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Butchering Patterns and the Implication for Hominin Feeding Behaviour at HWK EE in Olduvai Gorge, Northern Tanzania

by

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CERTIFICATION

The undersigned certify that they have read and hereby recommend for acceptance by the University of the Witwatersrand entitled: ***Butchering Patterns and the Implication for Hominin Feeding Behaviour at HWK EE in Olduvai Gorge, Northern Tanzania*** in fulfilment of the requirements for the MSc. Degree in Palaeontology of the University of the Witwatersrand, South Africa.

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DECLARATION

I, **Jackson Stanley Kimambo**, declare that this dissertation is my original work. It is being submitted for the Master of Science in Palaeontology at the University of the Witwatersrand, South Africa. This work has not been presented and will not be presented to any other University for a similar or any other degree award.

Signature

JSKimambo

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LIST OF ABBREVIATION

C-H-C: Carnivore-to-Hominin-Carnivore

CO: Carnivore Only

ESA: Early Stone Age

e.g.: Example

FLK: Frida Leakey Korongo

F-H-H: Felids-Hominin-Hyena

H-C: Hammerstone-to-carnivore

HWK EE: HenriettaWilfrida Korongo East

i.e.: That is

Ka: Thousand years

LAS: Lower Augitic Sandstone

MSH: Midshaft

MRT: Middle Range Theory

Mya: Million years ago

NCA: Ngorongoro Conservation Area

NISP: Number of Identified Specimens

OGAP: Olduvai Geochronology and Archaeology Project

V-H-C: Vulture-to-Hominin-to-Carnivore

WB-C: whole bone-to-carnivore

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ABSTRACT

Meat-eating by early hominins played an important role in the biological and cultural evolution of humans. Butchery marks such as cut and percussion marks are the direct evidence of meat-eating by early human ancestors, dating back to at least 2.6 Mya. However, the manner in which early hominins obtained carcasses, particularly during the Early Stone Age (ESA), is highly debated. While some researchers proposed hunting, others have suggested that early hominins were scavenging carcasses from large felids. Consequently, the two views have stimulated debate concerning the primary and secondary access of carcasses by the early hominins. The frequency of butchery and carnivore marks left on the faunal remains has been one the criteria used to understand the order of hominins' and carnivores' feeding on the carcass. Although there isa voluminous publication on this topic, the majority of them focus on a few sites due to a lack ofwell-preserved fossil remains. The recent excavation at the HWK EE site in Olduvai has revealed rich and well-preserved fossil remains with evidence of both carnivore and hominin modifications marks. Bone surface modifications (butchery, carnivore, and crocodile marks) were analysed using a 16x hand lens under strong light. These marks were recorded by a simple tally of absent or present and interpreted based on the established model of hominin feeding behaviours. The results of hominin butchery and carnivore modification marks demonstrate that hominins at the site exploited a range of small to large mammal taxa and a variety of carcass resources including meaty appendicular elements, crania, and ribs. The study also revealed that hominins at the site were selective on long bone depending on the quantity of marrow content for different taxa. The study of traces of butchery marks and percussion marks on the faunal sample support that hominins gained primary access to small mammals and secondary access to most of the medium and large mammals. These resources were likely obtained from large felids kills of carnivores such as lions and leopards. The study has also shown that in the absence of limb

elements, butchery marks on well-preserved ribs and crania elements can be used to infer the order of hominin access to carcasses. Moreover, the data also show that butchery patterns are consistent in both LAS and LEMUTA interval.

Chapter One

1 Introduction and Background Information

1.1 Introduction

The current study focuses on the analysis of hominin butchering patterns on faunal remains retrieved from the site of HenriettaWilfrida Korongo East East (HWK EE) in Olduvai Gorge, northern Tanzania. HWK EE is a late Oldowan site that has produced a well-preserved and large amount of lithic and fossil remains (Pante and de la Torre 2018; Pante *et al.,* 2018). The cultural sequence of the site indicates multiple occupations with a large amount of fossil and lithic remains recorded from the Lower Augitic Sandstone (LAS) and LEMUTA levels. Pante *et al.*, (2018) studied the faunal remains from the site to understand the carnivorous behaviour of late *Homo habilis* at Olduvai. These authors reported the presence of cut and percussion marks on the fossil remains. However, the frequencies and location of cutmarks on skeletal elements and the bone section on the fossil remains were not established. The frequency and distribution of hominin butchering marks contain important information about our early ancestors' feeding behaviour and interaction with the ecology. Cut and percussion marks, for example, are used to understand the sequence and order of carcass consumption of hominins (Blumenschine 1995; Domínguez-Rodrigo 1997a, b). Nonetheless, our current knowledge of early hominins' access to carcasses relies on referential and experimental studies, or samples from a few archeological sites such as FLK *Zinjanthropus* level and Bells Korongo (BK), due to the lack of well-persevered fossil remains or sampling biases (Blumenschine 1995; Domínguez-Rodrigo 1997a, b, Barr *et al.,* 2022). Potentially, HWK EE contains a large sample size that is well-preserved exhibiting traces of hominin feeding (Pante *et al.,* 2018). Thus, this study examined hominin cut and percussion marks on the HWK EE fossilsto understand hominins' access to carcasses at the HWK EE site.

1.2 Background Information

Early hominin ancestors left behind material that provides insightful information about their lifestyle and environmental adaptation. This cultural material includes but is not limited to fossils and lithic artefacts. While lithic artefacts provide the earliest evidence of human technological advancement, the faunal remains with traces of butchery marks including cut and percussion marks are the direct indications of hominin meat-eating (Leakey 1971; Bunn 1981,1982; Potts and Shipman 1981; Braun *et al.,* 2019). Archaeological evidence from Eastern African sites suggests that early hominins started to incorporate meat in their diet during the Early Stone Age (ESA) (Bunn 1981, 1982; Potts and Shipman 1981; Semaw *et al.,* 1997; de Heinzelin *et al.,* 1999). The earliest evidence of meat-eating thus far comes from the site of Gona in Ethiopia, dating to around 2.6 Mya (Semaw *et al.,* 1997; de Heinzelin *et al.,* 1999). The evidence of early hominin meat-eating recovered from archaeological sites has attracted discussion among many paleoanthropologists. For instance, the manner in which hominins acquired and processed carcasses during the ESA is hotly debated (e.g., Bunn 1981, 1982; Bunn and Kroll 1986; Binford 1981; Blumenschine 1987, 1988, 1991, 1995; Domínguez-Rodrigo 1997a; Domínguez-Rodrigo*et al.,* 2009; Pante *et al.,* 2012, 2018). The presence of both hominin modification marks (e.g., cut and percussion marks) and carnivore-inflicted tooth marks are the main reason for this debate (e.g., Blumenschine 1988; Domínguez-Rodrigo 1997a; Domínguez-Rodrigo*et al.,* 2009, Pante 2010; Pante *et al.,* 2012, 2018).

Faunal remains with carnivore-induced modification marks are sometimes recovered from Eastern African hominin-bearing sites (e.g., Leakey 1971; Bunn 1981, 1982; Domínguez-

Rodrigo*et al.,*2009; Pante *et al.,* 2018). Some specimens exhibit a combination of carnivore and hominin modification marks (e.g., Bunn 1981; Pante *et al.,* 2018). A question that remains unanswered is whether or not hominins transported skeletal elements to the campsite associated with flesh and marrow content (e.g., Binford 1981; Blumenschine 1987, 1988; Domínguez-Rodrigo1997a). An attempt to disentangle this question has resulted in conflicting interpretations of hominin feeding behaviour among various scholars (e.g., Blumenschine 1995, Domínguez-Rodrigo 1997a, b). The debate is on the interpretation of the frequency and location of cut marks on the carcass skeletal elements (Bunn and Kroll 1986; Domínguez-Rodrigo 1997; Bunn 2002; Binford 1981, 1984, 1988; Blumenschine 1988. 1995; Bunn 2001).

Bunn (1981) and Pots and Shipman (1981) first reported the evidence of cut and percussion marks on fossil remains recovered from the FLK *Zinjanthropus* level in Olduvai, northern Tanzania, and FxJj50 in Koobi Fora in northern Kenya. These assemblages also exhibited traces of carnivore modification marks (Bunn 1981. Bunn’s (1981: 576). Bunn’s (1981: 576) interpretation of the fracture patterns and the cut marks on faunal remains from the FLK *Zinjanthropus* level suggested that early hominins were feeding on carcasses containing a substantial amount of tissue. Bunn (1982, 2001), Bunn and Kroll (1986), and Domínguez-Rodrigo (1997a, 1999) link the high incidence of cut marks on a carcass skeletal element with hominins having primary access to a carcass with a substantial amount of meat obtained through hunting or power scavenging.

Conversely, Binford (1981, 1988), as well as Blumenschine (1988, 1995), argued that hominins at FLK *Zinjanthropus* level were scavenging their meat resources from large carnivore kills, having secondary access to a partially de-fleshed carcass. Binford (1981) further adds that hominins of the FLK *Zinjanthropus* level had access mainly to non-meaty and low-utility bones.

Thus, a high incidence of cut marks on the skeletal elements is associated with hominins removing a scrap of meats from the carcass (Binford 1981, 1986, 1988; Blumenschine 1988, 1995).

From the 1980s, Blumenschine conducted a series of actualistic studies to develop models for interpreting the order and the sequence of access to carcasses by hominins (Blumenschine 1986, 1987, 1988, 1995). After Blumenschine work, other scholars (e.g., Pobiner 2005, Gidna 2015) have also conducted actualistic studies to test hominin carnivory feeding behaviours. When the results derived from Blumenschine actualistic studies were compared to the fossil record at the FLK Zinj site, the frequency of hominin and carnivore-induced marks suggest that early hominins were scavenging de-fleshed carcasses from felid kills (Blumenschine 1987, 1988; Blumenschine and Selvaggio 1988). Further, according to Blumenschine (1986, 1991), the cut marks observed on the fossil remains were produced when hominins were removing scraps of meat from the bones.

Domínguez-Rodrigo (1997a) countered Blumenschine interpretation in support of Bunn (1981). Domínguez-Rodrigo's (1997a) interpretation is derived from a series of experiments to understand felid carcass consumption and the amount of flesh left after the carcasses are discarded by carnivores. One goal of his study was to test Blumenschine’s hypothesis that early hominins had access to the carcass in a de-fleshed state by large carnivores. According to Domínguez-Rodrigo(1997a), large carnivores leave a significant amount of meat on skeletal elements after feeding, and that the process of removing this flesh leaves behind butchery marks caused by hominins, resulting in cut marks on the bone surface. He compared his experimental results with those of the FLK *Zinjanthropus* level and concluded that early hominins at the site had access to carcasses containing considerable meat content.

Several possible explanations are contributing to the above discrepancies. First, Domínguez-Rodrigo(1997a) applied different methods and analytical procedures from those applied by Blumenschine (1995). Domínguez-Rodrigo (1997a), for example, did not conduct a controlled experiment. Whereas experiments were done (Domínguez-Rodrigo 1997a), it does not reflect the realistic carnivore feeding process. For example, Domínguez-Rodrigo (1997a) included an analysis of cow legs that were collected before the lion had completed the feeding process. According to the author, the carcass was collected after the Maasai chased away the lions which were feeding on the carcass (Domínguez-Rodrigo 1997a). The author asserts that:

"…. To get a complete picture of cut-mark patterns on human-made bone assemblages, subsequently ravaged by scavengers, I used the right limbs of a cow killed by two lions in Kulalu near a Maasai camp in August 1995. They were almost completely intact (with the flesh mostly untouched), as the lions had eviscerated the carcass and consumed most of the two left legs, before being chased away from the prey" ……. (Domínguez-Rodrigo 1997a: 675). With regards to this explanation, it is not imaginable that the author reports a significant amount of flesh left by felids on the carcass. Blumenschine (1995: 33) has shown that the comparability and the logic of experimental and archaeological data would match if the control samples are comparable in the process of bone fragmentation and their resulting features.

The analytical method is another potential factor that has caused different interpretations of the fauna generated from actualistic and those recovered from the hominin-bearing sites. For example, Pante (2010) pointed out the statistical discrepancies resulted in a different interpretation of the FLK *Zinjanthropus* level fossil remains (also see Pante *et al.*, 2012). According to Pante (2010: 22), parametric statistics were employed to describe nonparametric hominin feeding models. According to Pante *et al.*, (2012: 396), the models are nonparametric because each model was developed from a small number of fauna (groups of bones from a single individual and feeding episode/experimental trial), among which proportions of various feeding traces are not normally distributed. Pante *et al*., (2012) used the bootstrap statistical analysis method to refine and validate the sequence of feeding behaviour observed from experimental and fossil remains. Nonetheless, the finding of his study corroborates results generated by Blumenschine (1988) and Capaldo (1995) (Pante 2010: 36).

Studies by Blumenschine (1987, 1988, 1995) and Blumenschine and Selvaggio (1988) have thus far provided a comprehensive framework to assess the sequence and order of hominin and carnivore feeding on a carcass. The frequency of cut, percussion, and carnivore tooth marks on the skeletal element and portion provides an important signal regarding which agent acted first on the carcass (Blumenschine 1988, 1995). Also, percussion marks on fossil remains are evidence that hominins transported long bone portions to the sites to extract bone marrow (Bunn 1982; Blumenschine 1988, 1995; Blumenschine and Selvaggio 1988). The incidence of percussion and tooth marks on the skeletal portion determines the primary or secondary access to the long bone portion of the carcass (Blumenschine 1995). This criterion has been used and successfully replicated on fauna material from FLK *Zinjanthropus* level (e.g., Blumenschine 1988; 1995; Blumenschine and Selvaggio 1994a, b; Selvaggio 1998; Pante *et al.,* 2012).

Although a substantial number of actualistic studies and referential frameworks on hominin primary and secondary access to carcasses have been established based on traces of butchering patterns and carnivore modification marks, their implications for hominin feeding behaviour are known from only a few archaeological/palaeoanthropological sites. This is because faunal remains from archaeological sites are limited in number and the majority lack a good state of bone surface preservation (Blumenschine *et al.*, 1994b: 199). For example, at the Olduvai site, the FLK *Zinjanthropus* level site has been a center of this debate (e.g., Domínguez-Rodrigo 1997a; Pante 2010; Pante *et al.,* 2012). Very recently, Domínguez-Rodrigo*et al.,* (2009) expanded this discussion to the Bell Korongo site (BK), located in Olduvai Gorge, Tanzania. This discussion is further expanded in this study focusing on a well-preserved faunal remains from HWK EE in Olduvai Gorge, northern Tanzania.

As noted earlier, the HWK EE fossil remains preserve a rich and complex hominin feeding repertoire (Pante *et al.,* 2018). Therefore, traces of hominin butchering marks, namely cut and percussion marks, and carnivore tooth marks are used in this study to examine whether or not the locations and incidences of cut marks on the HWK EE fossils are consistent with hominins having primary or secondary access to carcasses, what carcass parts were hominins mostly interacting with, and what does this suggest about their feeding behaviour.

1.3 Research Hypothesis

Butchery and carnivore-induced marks on the skeletal elements reflect the order of hominin access to a carcass at the HWK EE site.

1.4 Testing Implication

Count of butchery and carnivore marks on skeletal elements and sections on HWK EE reflect the order (primary and secondary access to a carcass) of the hominin feeding sequence.

1.5 Objectives of the Study

The main objective of this study was to examine the butchery patterns on the fossil remains from HWK EE and to investigate their implications for hominins feeding behaviour during Oldowan times in Olduvai Gorge, northern Tanzania. More specifically, my study was aimed at:

i. Examining whether the locations and incidences of cut marks on the HWK EE fossils are consistent with hominins having primary or secondary access to carcasses,

ii. Investigating if hominins butchery patterns are consistent across the LEMUTA and LAS and

iii. Studying the carcass parts that were exploited by hominins and determining what this suggests about their behaviour.

1.6 Research Questions

i. Are the locations and incidences of cut marks consistent with hominins having primary or secondary access to carcasses?

ii. Are the butchery patterns consistent across the LEMUTA and LAS?

iii. Which carcass parts did hominins most often exploit and what does this suggest about their behaviour?

1.7 Study Area

This study focuses on faunal materials excavated from HWK EE in Olduvai Gorge, northern Tanzania. Olduvai Gorge is on average 100 meters deep, cutting across a 50-kilometer-wide rift platform basin located between Precambrian basements to the west and the Plio-Pleistocene Ngorongoro Volcanic Highland to the east (Hay 1976; Ashley 2002). The gorge lies on the eastern flanks of the Ngorongoro volcanic highland in the Ngorongoro Conservation Area (NCA), on the plains of the Serengeti ecosystem (Hay 1976).

The present-day Olduvai Gorge exposes a two-million-year sedimentary record in an incised river valley draining eastward from the Serengeti Plains (Hay 1976; Ashley 2002). The uplift of volcanic highlands to the east and south formed the Olduvai Basin about 2.0 Ma and down-cutting stream activity over the past 200 thousand years (ka) eventually created the modern gorge, which splits into two fingers, the Main and Side Gorges. HWK EE is in the southeast part of the Junction Area (Figure 1) at Olduvai Gorge (de la Torre *et al.*, 2018a, b).

The palaeontological significance of the Olduvai Gorge was first recorded in 1911 by German entomologist, Prof. Wilhelm Kattwinke (Leakey 1965, 1971; Hooijer 1975). Kattwinke reported and collected fossilised bones of an extinct three-toed horse (*Hipparion "stylohipparion")* that was eventually translocated to the Berlin Museum (Leakey 1965, 1971; Hooijer 1975). These fossil remains attracted other scholars including Dr. Hans Reck, who briefly described the geology of the area between 1913-1914 and collected additional palaeontological and hominin fossils (Leakey 1965, 1971). After Dr. Reck, Louis Leakey visited Olduvai Gorge in the 1930s and he was the first scientist to notice the evidence of simple and crude stone tools at the site of FLK (Leakey 1951, 1965). He subsequently named them Oldowan tools. Leakey's visitation and the discovery of the stone tools, fossils, and later, hominin remains, was the turning point in palaeoanthropological research at Olduvai Gorge (Leakey 1951, 1959, 1961, 1965). To date, the area has attracted scholars from across the world and more importantly, it has produced remarkable evidence to understand hominin biological, cultural, and technological evolution (Leakey 1971; Njau 2020).

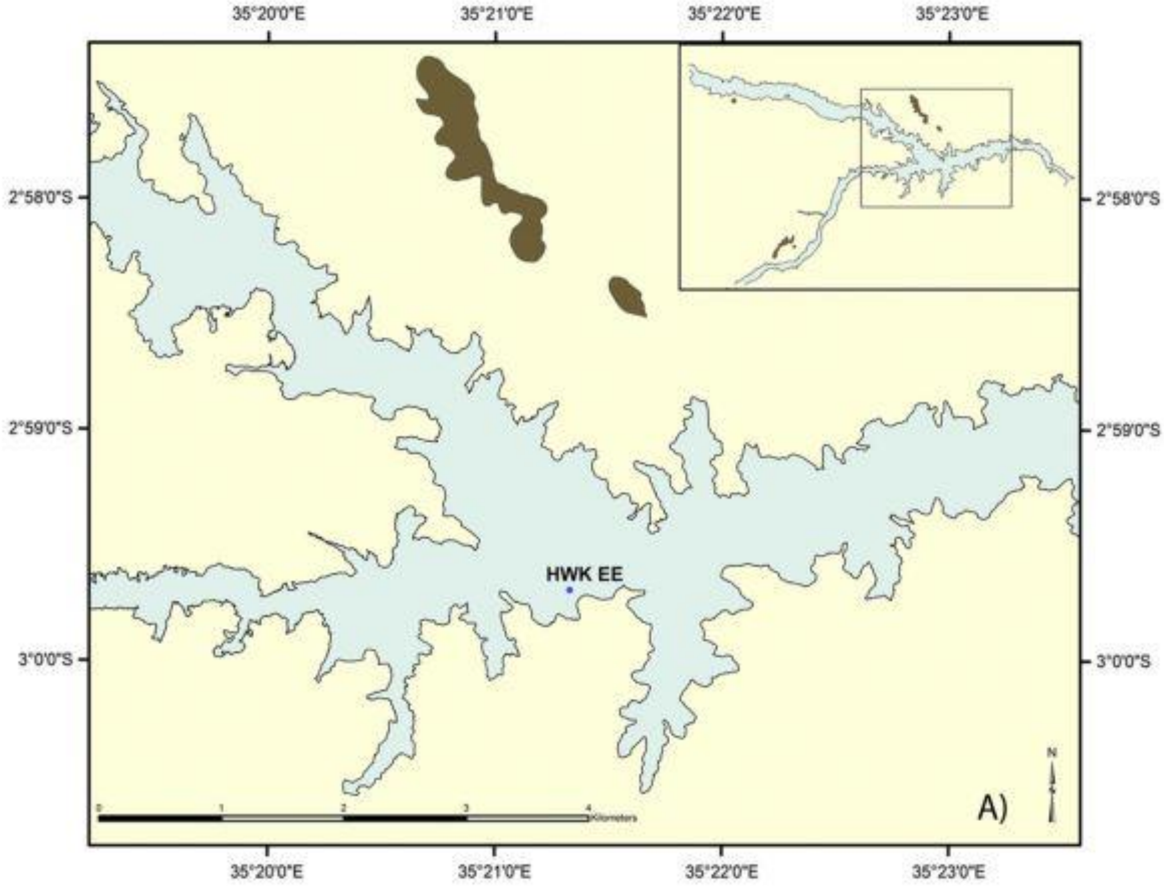


Figure 1: Map of Olduvai Gorge showing the location of HWK EE

Source: Pante and de la Torre 2018.

1.7.1 Site Description

1.7.1.1 Previous Fieldwork

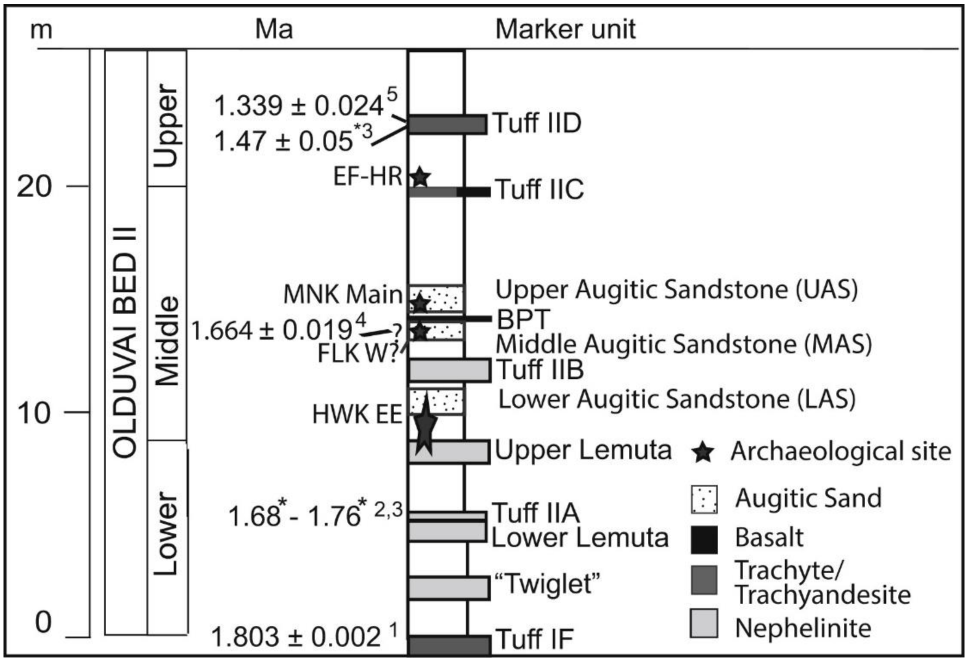
The initial archaeological excavation of the site was done by Mary Leakey in the 1970s (Pante and de la Torre 2018; Pante *et al.,* 2018). Leakey's excavation recovered over 2902 lithics and 1569 fossil specimens. However, none of these materials were systematically studied at the time. In 2008, the Olduvai Geochronology and Archaeology Project (OGAP) launched a study to re-examine the origin of Acheulean technology at Olduvai Gorge, Tanzania (de la Torre *et al.,* 2012), and for the first time, Leakey's collection was systematically analysed as part of the OGAP project (Pante and de la Torre 2018). In 2009, OGAP revived excavation at the site which expanded the amount of lithic artefact and faunal materials, and these remains have been extensively studied (de la Torre *et al.*,2018a; Pante *et al.*, 2018; Pante and de la Torre 2018 and reference therein). The OGAP collection from HWK-EE encompasses material recovered from four trenches (but see de la Torre *et al.*, 2018a for more details).

1.7.1.2 Geological and Cultural Sequence of the Site

HWK EE is a Bed II site in Olduvai Gorge, Tanzania (Leakey 1971; Pante and de la Torre 2018). Bed II is of special interest because of its many lithofacies and environments (Hay 1976). Bed II is divided into Lower, Middle, and Upper Bed II (Hay 1976; McHenry and Stanistreet 2018). This sequence is further subdivided into a series of tuffs (Tuffs IIA-Tuff IID) and different lithological phases including the Lower and Upper LEMUTA as well Lower, Middle, and Upper Augitic Sandstone (McHenry and Stanistreet 2018). Bed II is particularly important from the standpoint of archaeologists because it contains numerous sites representing ESA industries: Oldowan (Lower Bed II), Developed Oldowan, and Acheulian (Middle and Upper Bed II). Furthermore, Bed II has also provided evidence of early humans such as *Homo habilis* and *Homo erectus* (Hay, 1976; Pante and de la Torre 2018; Pante *et al.*, 2018). HWKEE is a late Oldowan site at Olduvai Gorge (Pante and de la Torre 2018; McHenry and de la Torre 2018; de la Torre *et al.*, 2018; McHenry and Stanistreet 2018). It is stratigraphically positioned just before the appearance of Acheulean technology at Olduvai, and it is constrained between Tuffs IIA (1.677 ± 0.03 Ma) and Tuffs IIB immediately above the boundary between Lower and Middle Bed II, dating to 1.7 Mya (Pante and de la Torre 2018; McHenry and de la Torre 2018; de la Torre *et al.*, 2018a, b; McHenry and Stanistreet 2018). The site represents multiple occupations by hominins and carnivores (Pante *et al.*, 2018). The fossils and lithic remains are abundant in LEMUTA and

LAS levels (Pante *et al.*, 2018). Figure 2 shows the stratigraphic section of Bed II and the position of the HWKEE site.

Figure 2: Stratigraphic section of Bed II and position of HWK-EE



Source: McHenry and Stanistreet 2018.

1.8 Theoretical Framework

Palaeoanthropologists make inferences about past human behaviours through the utilisation of modern analogies. This approach is rooted in the concept of Middle Range Theory (MRT), commonly used in sociological studies (Binford 1981). MRT is an important tool for paleoanthropologists to establish the link between static traces observed in the fossil record and its associated dynamic past human behaviours. When applying MRT to paleoanthropological contexts, one should connect it to the principle of uniformitarianism (Blumenschine *et al.*,1994). The fundamental assumption of the latter is that the present is the key to the past. That is, the present-day natural phenomena such as volcanic eruptions, floods, and climatic changes are well preserved in the geological records, and these are uniform events and key factors for shaping the landscape, ecology, and life history throughout the geological sequence. MRT operates in the same manner. It bridges the gap between what happened in the past through the modern process related to the creation of archaeological, paleontological, or geological records and its associated traces resulting from the whole process which created them (Binford 1962, 1981; Blumenschine *et al.*, 1994; Fagan and Nadia 2016).

Fossil remains from archaeological sites are limited in number and the majority are in a poor state of preservation (Blumenschine *et al.*, 1994: 199). Moreover, these remains contain unchanging signs of various past cultural, biological, and natural dynamics caused by different actors. No one witnessed who or what created the static marks on fossils recovered from the archaeological record (Binford 1962, 1981; Blumenschine *et al*., 1994). Thus, palaeoanthropologists use additional lines of evidence to construct these prehistoric behavioural repertoires by using MRT (Binford 1962, 1978, 1981). These behavioural patterns are often visualised through controlled actualistic studies which are either through naturalistic or experimental approaches. On the one hand, the naturalistic involves the study of modern animal (ethology) and human (ethnography) behaviours (Binford 1962, 1978; Blumenschine 1987, 1988, Blumenschine *et al.*, 1994; Selvaggio 1994, 1998). On the other hand, the experimental approach involves a simulation of various past human activities such as the uses of stone tools for butchering carcasses to construct past human behavioural patterns associated with these activities (Jones 1980; Toth 1985; Blumenschine 1995; Leenen 2011, Merritt 2012, 2017; Merritt and Davis 2017).

Actualistic and controlled experiments (e.g., Blumenschine 1988, 1995; Blumenschine and Selvaggio 1988; Selvaggio 1994a, b; Capaldo 1995) have established important criteria to evaluate the feeding behaviour of early hominin ancestors. The current study will use the framework established from these studies to explore hominin feeding behaviour at the HWK EE site in Olduvai Gorge, northern Tanzania.

1.9 Dissertation Organisation

This dissertation is divided into five chapters. Chapter one of this work has introduced the research topic, research problem, the objectives of the study, and research questions. It has also presented the study area of the study covering geographical location, previous research work as well as a geological and cultural sequence of the site. The theoretical framework that guides this study is also presented in this chapter. Chapter two of this study provides a literature review. The chapter is divided into three sections starting with the general introduction, taphonomy, and empirical studies related to this study. Chapter three entails detail about the data collection process and how they were analysed. Chapter four present the results of the findings, while chapter five presents the discussion of the finding and conclusion.

Chapter Two

2 Literature Review

2.1 Introduction

Zooarchaeological and taphonomic studies of Plio-Pleistocene sites in Africa have revolutionised our understanding of the meaning and function of early archaeological sites (Brain 1981; Lyman 1987; Potts *et al.,* 1987; Blumenschine and Selvaggio 1988; Peters and Blumenschine 1995). This involves the studies of hominin and carnivore modification marks, lithic assemblages, and other natural and biotic site-formation processes. Since the discovery of the first evidence of stone tools and faunal assemblages from archaeological sites (Leakey 1951), palaeoanthropologists have been curious to understand, among other things, how early hominins exploited meat resources and their interaction with their surrounding environments. This chapter reviews the literature related to this study. The chapter is divided into three sections. The goal of this study is to examine hominin feeding behaviour based on traces of butchery marks left on the fossil remains recovered at HWK EE. It should, however, be noted that fauna remains from archaeological sites contain several taphonomic signatures that must be addressed. For this reason, the first section of this chapter provides the general background of the taphonomic process that affects bone surface modification. Section two reviews various literature on hominin hunting *vs.* scavenging or primary and secondary access of carcasses by hominins during the Oldowan time. In this section, an experimental/referential framework established to understand hominin feeding behavior is also discussed.

2.2 Taphonomy

Fossil remains recovered in archaeological and palaeontological sites represents organisms that died and were preserved for thousands or millions of years. No witness survives to narrate their cause of death and experience (Brain 1981: 3). These fossil remains contain traces of natural, biotic, and anthropogenic processes that affect an organism from the time of death to the time of recovery (Lyman 1994). The study of bone surface modifications such as cut, chop, and percussion marks, carnivores modification marks, weathering, and trampling provide clues to understanding the broad perspective of what may have happened to an organism and site formation processes (Isaac 1978; Brain 1981; Lyman 1994; Blumenschine 1988, 1995). This detective work is known as taphonomy, a branch of palaeontology that deals with the laws of burials (Brain 1981; Lyman 1994).

A record of taphonomic agents and processes affecting animal remains is called a *taphonomic history* or *taphonomic pathway* (Lyman 1994; Reitz and Wing 1999, 2008). The history of a fossil or fauna material recovered from an archaeological site began when an animal was acquired, killed, and exploited. These materials are discarded and deposited (biostratinomy) and thereafter subjected to diagenesis (Reitz and Wing 1999, 2008). Determination of taphonomic history is frequently used by zooarchaeologists to determine taxa that were exploited by hominins and the relative proportion in which they were exploited (Lyman 1994: 6). In turn, this helps to develop different interpretations regarding hominin feeding behaviour (Lyman 1994).

Taphonomic investigations of faunal material from archaeological sites have also assisted to identify various agents responsible for causing traces of bone surface modification. For instance, micro-invertebrate organisms modify bones in several ways (Blumenschine *et al.,* 2006; Backwell *et al.,* 2012), and bioerosion on bone surface modifications are caused by marine invertebrates or insects. These modifications are either mechanical or chemical (Blumenschine *et al.,* 2006). Insects and particularly termites (*Trinerviterme strinervoide*), for example, induced various modifications on bone surfaces. These include, but are not limited to surface pits, starshaped marks, clusters of sub-parallel striations, multiple parallel incisions along edges, and boreholes (Backwell *et al.,* 2012). Furthermore, algae, fungi, and bacteria can affect and stain bone surfaces (Domínguez-Rodrigoand Barba 2006). These microorganisms cause stains on the bones that have been mistaken for carnivore tooth marks on fossils assemblage (Blumenschine *et al.,* 2006).

Carnivores including hyena (*Crocuta, Hyaena hyaena, Hyaena brunnea*) and leopard (*Panthera pardus*) modify and accumulate bones (Brain 1981; Haynes 1983; Blumenschine 1986, 1988; Pobiner and Blumenschine 2003; Faith *et al.,* 2007), and evidence of their activities has been recovered in hominin-bearing sites (Brain 1981; Cavallo and Blumenschine 1989; Pickering 1999, Pickering 2002; Sauque *et al.,* 2014). According to Aziarra *et al.,* (2016, 2017), lions (*Panthera leo*) are also a potential agent of bone accumulation. The patterns and degree of carnivore modification vary depending on the type of carnivore species as well as the type and size of a carcass (Haynes 1980: 341; Pobiner and Blumenschine 2003: 118). For instance, hyenas cause a high degree of damage to animal bones because they have powerful jaws to crush bones (Cruz-Uribe 1991; Pickering 2002). This allows them to destroy parts or an entire skeletal portion during feeding (Brain 1981; Haynes 1983; Blumenschine 1987; Binford *et al.,* 1988; Marean 1991; Pickering 2002).

On the other hand, lions, leopards, and cheetahs (*Acinonyx jubatus*) cause minimal damage to a carcass (Brain 1981; Blumenschine 1987). Unlike hyenas (bone crunchers), lions are flesh eaters and as such, they leave few tooth marks on bones (Selvaggio 1994; Pobiner 2007). Haynes (1983: 169) assert that African lions do not sustain gnawing on large mammal bones. However, gnawing is occasionally caused by captive adults and cubs (Haynes 1983). This observation is confirmed by other studies (Pobiner 2007; Parkinson *et al.,* 2015, Gidna 2015). Among other induced modification marks, large cats produce relatively deep identifiable grooves shaped by their carnassial and other cheek teeth cups. Haynes (1983: 169) indicates that when these grooves are produced, they are often larger than grooves inflicted by teeth of hyenas or wolves. Selvaggio (1994) has shown that carnivore fossils are scarce in the fossil record. As a result, traces of carnivore modifications during Oldowan times relies on their induced surface modifications. For example, at the site of FLK, some tooth marks are attributed to large felids, but their fossil remains have never been recovered in sediments from Bed I (Leakey 1965).

Other than carnivores, porcupines, raptors, and vultures also accumulate and modify bones. This is exemplified by work undertaken in South African cave sites (e.g., Dart 1957; Brain 1981; Lyman 1994; Hutson 2006). Porcupines can transport large quantities of bones to caves or their lairs. Porcupine gnaws bones to wear down their incisors that grow throughout their lifespan and obtain mineral salts (Brain 1981: 109). Raptors such as owls roost and nest close to the entrance of caves or rock shelters that contain archaeological remains (Brain 1981: 118). During the daytime resting, owls regurgitate pellets comprising indigestible remnants of pray (Brain 1981). Apart from accumulating bones in rock shelters and cave sites, vultures also scavenge carcasses hunted by large carnivores. During their scavenging activities, vultures leave their modification marks on bone surfaces (Binford *et al.,* 1988; Reeves 2009). They also provide signals for other scavengers like hyena and hominin to locate a carcass (Blumenschine 1987; Blumenschine and Cavallo 1991; Pante *et al.*, 2012, 2018).

Early hominins played a substantial role in various palaeoanthropological site formations. They transported, accumulated, and modified both faunal and stone objects (Leakey 1971, Bunn 1981, 1982; Lyman 1994, Pante *et al.,* 2018). Butchery marks on animal bone recovered from archaeological sites are the primary evidence of hominin feeding activities (Bunn 1981; Potts and Shipman 1981; Selvaggio 1994, Pante *et al.,* 2012). McPherron *et al.,* (2010) reported evidence of butchery marks on fossil remains dating to 3.39 Mya at the site of Dikika in Ethiopia. These butchered marks are proposed to be the earliest evidence of hominin meat consumption (McPherron *et al.,* 2010). However, this is a highly debated topic (e.g., Domínguez-Rodrigo *et al.,* 2011, 2012; Thompson *et al.,* 2015). Some researchers (e.g., Domínguez-Rodrigo *et al.,* 2011, 2012) suggested that the Dikika marks were produced by animal trampling or incidental movements. Thus, the earliest accepted evidence of hominin butchery of large mammals comes from the site of Gona in Ethiopia, dating to 2.5 Mya (Semaw *et al.,* 1997; de Heinzelin *et al.,* 1999). At Olduvai, sites such as FLK Zinj, FLKN level 1-2, DK level 3, and HWKEE, bones with evidence of hominin-induced butchery marks were found in sediments dating to between 1.85 and 1.71 Mya, contemporaneous with the Oldowan industry, *Homo habilis* and *Paranthropus boisei* (Leakey 1959, 1961, 1966, 1971; Leakey *et al.,* 1964; Blumenschine *et al.,* 2003, Pante *et al.,* 2018). These results have offered a unique insight into early hominin feeding behaviour and their capacity to process carcasses during the ESA (Bunn 1981, 1986; Blumenschine 1995).

Notably, small to large mammal-sized fauna remains recovered from the ESA context at Olduvai Gorge contain evidence of butchery marks suggesting that these mammals contributed to the diets of hominins (Leakey 1971; Pante *et al.,* 2018). One of the main questions developed from these remains is which agent accumulated these faunal remains or whether early hominins hunted or scavenged and otherwise obtained fleshed or de-fleshed carcasses from large predators. This topic has caused debate among paleoanthropologists (Binford 1981; Binford and Stone 1986; Brain 1981; Bunn and Kroll 1986; Binford *et al.,* 1988; Blumenschine 1988; Selvaggio 1994; Faith *et al.,* 2007; Pante *et al.,* 2012). HWK EE is an important site as it may represent one of the last sites associated with *Homo habilis* before the appearance of *Homo erectus* and Acheulean technology at Olduvai Gorge (Pante *et al.*, 2018). The site has produced well-preserved fossil remains revealing a rich record of feeding traces left by hominins, carnivores, crocodiles, and vultures that can help to broaden our understanding of early hominin foraging behaviour (Pante and de la Torre 2018; Pante *et al.*, 2018). The subsequent section reviews various literature relating to hunting *vs* scavenging, or hominin primary and secondary access to carcasses.

2.3 Hominin Hunting *vs.* Scavenging Debate

The hypothesis of how early humans obtained food (meat resources in particular) was suggested about two centuries ago. Chief amongst the pioneer of this idea is Charles Darwin (Darwin 1871). In his book, *The Decent of Man, and Selection in Relation to Sex,* Darwin (1871) visualised human development from lower to higher forms and suggested various factors that enabled humans to interact with the ecology. For instance, Darwin (1871: 137) wrote that: '…through his powers of intellect, articulate language has been evolved; and on this, his wonderful advancement has mainly depended. He has invented and is able to use various weapons, tools, traps, &c., with which he defends himself, kills or catches prey, and otherwise obtained food'. To paraphrase Darwin's statement in the context of the current study, humans invented tools and were able to use such tools to kill or catch prey. If this interpretation is correct, then Darwin (1871) was referring to the hunting ability of humans from early forms. However, Darwin's ideas did not have sufficient evidence from the early hominin-bearing sites. Nonetheless, it is in this paradigm that subsequent studies viewed humans as a hunter.

The discovery of the Taung child in 1924 and associated fauna material from South Africa expanded the discussion about the hunting ability of early hominins to obtain meat resources (e.g., Dart 1925, 1926, 1949, 1957). The Taung child is the species of Australopithecine (*Australopithecus africanus*) dating to between 3.3 and 2.6Mya (Herries *et al.*, 2013). The site, where the Taung child was found, also yielded other fauna material including bovids, carnivores, and primates to mention a few. However, no evidence of stone tools was found associated with the *Australopithecus africanus* deposit (Dart 1925, 1949, 1957). Amongst the fauna remains collected from the Taung deposit, Dart (Dart 1949, 1957) noted that baboon skulls exhibited unusual surface modification. He described these surface modifications as radiating fractures in the right parietal of the temporal region, and a rounded opening in the vortex or base of skulls. Dart (1949: 3,1957) proposed that the radiating fractures were inflicted by sharp objects, possibly stone tools. He then associated these damages with dexterous force and violence of the actor (Dart 1949: 3, 1957).

Further analysis of the surface modification on fauna material from the Taung deposit led Dart (1957) to suggest that selected mammals' long bone portions, mandibles associated with teeth, and horns were used by hominins to inflict damage. This interpretation led to the foundation of the “Osteodontokeratic” hypothesis. Dart (1957) viewed *Australopithecine africanus* as a hunter, assisted with bone, teeth, and horns as tools for, among other things, hunting and processing meat resources. Although Dart (1957: 10) summarised the archaeological evidence for bone tools as was known at the time, none of the bone tools were recovered from early hominin-bearing sites. Thus, Dart was among the first scientists to propose that early hominins, particularly members of the australopithecines, were hunters. This interpretation remained undisputed until the 1970s (Brain 1981).

The later extensive taphonomic work carried out in the South African caves by C.K. Brain, the then paleontologist at the Transvaal Museum provides a comprehensive history of cave site formation processes (Brain 1981). In his seminal book, *The Hunters or the Hunted?* (Brain 1981), has revolutionised the interpretation of cave taphonomy in Africa. Brain (1981) refuted the *"*Osteodontokeratic*"* hypothesis by considering different variables related to site formation processes through the study of modern carnivore modification marks and ethnographic materials. For instance, it is now accepted that multiple agents such as leopards and porcupines were responsible for accumulating and modifying bone found in South African caves. Some of the hominin skulls such as SK54 and SK 349 (both belonging to *Australopithecines* members) from Swartkans Cave display modification caused by carnivores on the parietal bones (Brain 1970, 1981: 266-267). These modifications mark fit precisely with leopard canines, suggesting that hominins and other associated animals were hunted, and carnivores were responsible for bone accumulation in the cave (Brain 1970: 116-117, 1981: 266).

Brain (1967a, b,1969, 1970, 1981) also describes taphonomic biases that resulted in the misinterpretation of bones that were regarded as bone tools in cave sites. As stated earlier, Dart (1949, 1957) proposed that selected long bone elements, horns, and teeth were used by *Australopithecine* hominins to process carcasses (Dart 1949; 1957). However, Brain (1967b: 98, 1981) shows that fauna remain discarded on the sand in an arid environment, then affected by chemical weathering, and subsequently, followed by animal trampling produces a smooth surface on the bones that can be mistaken as bone tools. This interpretation contradicts Dart's (1957) views on the *Osteodontokeratic* culture. It was also noted that the density of bone affects the survivorship and faunal representation in the archaeological record (Brain 1981). Brain (1970, 1981) used these lines of evidence to refute the *Osteodontokeratic* hypothesis.

Although the *Osteodontokerati*c hypothesis was disputed by the 1980s, the debate about the hunting or scavenging behaviour of early hominin was not over. From the 1930s, more archaeological sites bearing hominin fossils, stone tools, and faunal remains were discovered in the East African rift valley system (e.g., Leakey 1959, 1971; Isaac 1967). Some of these sites are in Omo and Middle Awash found in Ethiopia, Koobi Fora and Turkana Basin in northern Kenya, as well as Olduvai and Laetoli sites in northern Tanzania. Of particular interest was the discovery of the FLK *Zinjanthropus* site in the Olduvai Gorge. FLK *Zinjanthropus* is a Bed I site dating to 1.8 Mya Leakey (1971). The site is widely known for producing ESA tools, faunal remains, and hominin fossils attributed to *Paranthropus boisei* and *Homo habilis* (Leakey 1959, 1960, 1965, 1971). Named after the first wife of Louis Leakey, Frida Leakey Korongo, the FLK *Zinjanthropus* site was discovered during Louis Leakey's first expedition to Olduvai in the 1930s. During this first expedition, faunal and lithic material were found scattered on the surface of the site. About 30 years later, in 1959, a hominin fossil of *Paranthropus boisei* (OH5) was found at the site (Leakey 1959). The discovery of OH5 marked the turning point for the expansion of the research area at the FLK *Zinjanthropus* site, resulting in the discovery of other hominin fossil remains such as *Homo habilis* associated with stone tools and faunal remains (Leakey 1960, 1962,1971).

Furthermore, excavation at the FLK *Zinjanthropus* site produced abundant faunal remains and lithic artefacts, distributed in different levels or sequences. Notably, both OH5 and *Homo habilis* were found in the same level associated with stone tools and fauna remains (Leaky 1959; 1960). Leakey (1971) described the concentration of faunal and lithic (Oldowan tools) material in this level as a living floor, where hominins would transport and share food resources. Elsewhere, names such as FLK *Zinjanthropus*, occupation level 22, Zinj floor, and Zinj level 22 have been used interchangeably to refer to the FLK living floor (e.g., Leakey 1971; Bunn 1981; Blumenschine 1995; Domínguez-Rodrigo1997; Domínguez-Rodrigo *et al.*, 2009).

The co-existence of two hominins (*Paranthropus boisei* and *Homo habilis*) species associated with stone tools and faunal remains at FLK *Zinjanthropus* fuelled several debates among palaeoanthropologists, including who made Oldowan tools, and the hunting *vs*. scavenging behaviour of Oldowan hominins (Leakey 1971; Bunn 1981; Blumenschine 1988; Susman 1991). The hunting *vs*. scavenging debate, the subject of this study, has lasted for over forty years. There are at least two schools of thought debating this matter. One group suggests that Oldowan hominins were hunters, or at least gained primary access to carcasses with a substantial amount of flesh using confrontational scavenging (e.g., Bunn 1981,1982, 1986; Bunn *et al*., 1983; Bunn and Kroll, 1986, 1988; Bunn and Ezzo 1993; Oliver 1994; Domínguez-Rodrigo1997, 2002; Domínguez-Rodrigo*et al.*, 2009, 2014; Domínguez-Rodrigoand Barba 2006). The second group suggests that Oldowan hominins were scavengers, who gained primary access to partially or de-fleshed carcasses from large felids through passive scavenging (e.g., Blumenschine 1986a, b, 1987, 1991, 1995, Blumenschine and Selvaggio; Binford 1988; Binford *et al.*, 1988; Cavallo and Blumenschine 1989; Blumenschine and Cavallo 1991; Blumenschine *et al.*, 1994, 1996, 2003, 2012;Selvaggio 1994, 1995; Capaldo 1995, 1997; Capaldo and Blumenschine 1994; Blumenschine and Selvaggio 1998; Pante *et al.*, 2018).

The faunal material from the FLK *Zinjanthropus* site was subjected to a detailed taphonomic study in the late 1970s by Bunn*et al.*, 1980and Potts (1981). Bunn *et al.*, (1980) and Potts and Shipman (1981) reported evidence of cut marks caused by hominins as well as carnivore marks on the fauna assemblage. Both cut and carnivore marks on the fossil remain provided unequivocal evidence that hominins and carnivores had access to the carcasses. However, the remaining question is who initially consumed the carcass and what line of evidence can be used to disentangle this aspect. Based on the distribution of cutmarks on different anatomical parts of the FLK *Zinjanthropus* faunal assemblage, Bunn (1981, 1983; Bunn and Kroll 1986) suggested that early hominins were efficient butchers using stone tools for skinning, dismembering, and de-fleshing substantial amounts of meat from carcasses. Skeletal parts representation and evidence of cutmarks on the faunal remains are the central basis of the argument by Bunn and Kroll (1986) of a hominin to carnivore feeding sequence. These authors are of the view that early hominins at FLK Zinjanthropus level had primary access to a carcass, which was then partially eaten by large predators (Bunn and Kroll 1986: 433, 440). Further, Bunn and Kroll (1986: 433) add that the scavenging carnivores such as hyenas and even small rodents were attracted to the bone remains after they have been accumulated by early hominins. This interpretation triggered the discussion about the Oldowan hominin hunting/scavenging behaviour, and primary or access to fleshed/de-fleshed carcasses at Olduvai Gorge.

Potts and Shipman (1981: 579) proposed that cut marks found on the fossil remains at the FLK *Zinjanthropus* site indicate hominins were exploiting carcass resources including meat, ligaments, and bone. They, however, caution that the evidence of cut marks neither provides evidence of the amount of flesh on the carcass, nor the hunting behaviour of early hominins. Bunn and Kroll (1986: 432) disagree with this view, arguing that Potts and Shipman (1981) used only a few samples to reach their conclusion. The Olduvai Gorge Oldowan assemblage, particularly from the FLK *Zinjanthropus* level, is characterised by low-utility skeletal parts such as metapodials (Leakey 1971; Bunn 1981, 1982; Bunn and Kroll 1986). Ethnographic studies focusing on modern hunter-gathersuch as the Hadza of the Eyasi Basin in northern Tanzania have played a vital role in testing early hominin hunting behaviour (e.g., Gifford 1977; Binford 1978,1981; Lupo and O’Connell 2002). Binford (1981) used the frequency of skeletal part representation derived from ethnographic studies to question the proposition of hunting behaviour by early hominins during the Oldowan period at Olduvai Gorge. He observed that the skeletal parts from sites in the Olduvai Gorge differ from those utilized by modern hunter-gatherers. Binford (1981) used this observation to argue that if early hominins were the initial consumers of the carcasses resulting from hunting, the assemblage would have been characterised by anatomical parts bearing a larger amount of edible tissue (also see: Binford *et al.,* 1988: 100). Binford *et al.,* (1988) further add that scavenging hyena tends to dislocate and remove bones from the kill site. Thus, this would have also affected the skeletal representation of the faunal remains at the site.

In response to Binford's 1981 argument that hominins were marginal scavengers, Bunn and Kroll (1986) used the s*chlepp* effect to describe the patterns of skeletal part representation based on the selective behaviour of transportation by hominins. Further, Bunn and Kroll noted that the Binford (1981) sample was subjective because it focused on the epiphysis portions and excluded mid-shaft portions. Alongside Binford's (1981) critique, Bunn and Kroll (1986: 440) also disagreed with Blumenschine's (1986) alternative interpretation of scavenging behaviour by early hominins based on naturalistic observations of carnivore feeding in the Serengeti and Ngorongoro National Park. Blumenschine (1986) proposed that Oldowan hominins were scavenging de-fleshed carcasses from large felids. Bunn's (1986) premature critique of Blumenschine's (1986) alternative interpretation of hominin scavenging behaviour was expected at the time. The reason for this is that the interpretation of hominin scavenging behaviour based on the fossil records was made without considering scavenging opportunities encountered by early hominins from a large predator such as lions (Blumenschine 1987: 383).

The actualistic and controlled observations of carnivore feeding behaviour (ethology) have produced significant information on the potential resources left by predators on carcasses (e.g., Blumenschine1986, 1987; Domínguez-Rodrigo *et al.,* 2009). For instance, scholars (Blumenschine 1986, 1987, 1988; Pobiner 2015) have shown that lion kills leave a few scraps of meat and bone marrow resources on a carcass. They, therefore, suggested that these would have been a potential scavenging resource for early hominins. In a similar vein, Cavallo and Blumenschine (1989: 396) noted that arboreal-cached leopard kills offer a frequent source of meat and marrow of small bovids. Thus, any opportunist diurnal hominin able to climb a tree would have been able to scavenge these resources without confronting any predators. Accordingly, Pante *et al.,* (2018) have reported that early hominins at HWK EE obtained a significant amount of flesh and marrow from small mammal sizes 1 (e.g., Dik-Dik) and 2 (e.g., gazelle).However, whether the frequency of butchery marks on the fossils remain aligns with hominin having primary or secondary access to the carcass was not tested.

Various models of hominin feeding behaviour have been derived from ethological and taphonomic studies (Blumenschine 1987, 1988; Selvaggio 1994a, b; Capaldo 1995,1997). These models have become a powerful tool to infer hominin feeding behaviour based on the fossils recovered from the archaeological site (Blumenschine1986, 1987; Selvaggio 1994a, b; Domínguez-Rodrigo *et al.,* 2009). Pante (2010: 25) as well as Pante *et al.,* (2012: 396) group these models into three groups, including one consumer, two consumers, and three consumers. A summary of these models and their implications for hominin behaviour is provided below.

2.4 Model of Carcasses Consumption and the Formation of Archaeological Sites

Quite often, faunal materials from Oldowan sites such as Olduvai Gorge and Koobi Fora display evidence of both hominin and carnivore-induced modifications (Bunn 1981, 1983, 1986; Selvaggio 1994; Pobiner 2007; Pante *et al.,* 2018). The sequence and incidences of hominin and carnivore modification marks are key factors for understanding the primary, secondary, or multiple accesses of hominins and carnivores to carcasses (Binford 1988; Selvaggio 1994, 1998; Blumenschine 1986, 1987; Pante *et al.,* 2012). This is determined through the proportion of the induced tooth, cut, and percussion marks on the bone surface produced during hominin and carnivore feeding activities (Blumenschine 1986, 1988, 1995; Pante *et al.*, 2012).

Several models representing single and multiple feeding sequences have been published to infer traces of hominins feeding behaviour and interaction with mammalian carnivores (e.g., Bunn 1981; Blumenschine 1988, 1995; Selvaggio 1994a, b; Blumenschine and Selvaggio 1998; Capaldo 1995, 1997).Because HWK EE faunal assemblages exhibit complex hominin and carnivore feeding behaviour, the general taphonomy of the assemblage was tested against five established feeding models describing primary and secondary access of carcasses by hominins. These include hammerstone only (HO); carnivore only (CO) models; the hammerstone-to-carnivore (H-C) model; the whole bone-to-carnivore (WB-C) model; and the vulture-to-hominin-to-carnivore (V-H-C) model (Pante *et al.,* 2018). The current study uses the same assemblage analysed by Pante *et al.,* (2018). Therefore, for consistency, the information generated from these models as summarised below provides the baseline for interpreting hominin feeding behaviour based on the frequency of butchery marks on the HWK EE faunal assemblage.

2.4.1 Carnivore-to-Hominin-Carnivore (C-H-C)

The C-H-C model provides inference where three agents are responsible for the modification of the carcass. This model explains that large felids first had preceded hominin access to a carcass, consuming all flesh but leaving a few scraps of meat and marrow resources. Then, hominins break the long bones to access bone marrow and finally discard them. Thereafter, hyenas consume grease-bearing cancellous bone and break most of the bones (Selvaggio 1994, 1998, Blumenschine 1995). According to Selvaggio (1994: 216), cut marks on skeletal parts are produced during the removal of flesh scraps, tendons, and the disarticulation of skeletal elements. The final assemblage is characterised by a large amount of mid-shaft portions, a high frequency of tooth marks on the epiphyseal fragments, and the absence of unmarked or percussion-marked on epiphyseal specimens (Selvaggio 1998).**Archaeological Implication:** Based on the sequence and features provided above, Selvaggio (1998),as well as Blumenschine (1995) as well as Pante *et al.*, (2012) have referred to the FLK *Zinjanthropus* faunal assemblage as a C-H-C feeding sequence (Selvaggio 1994, 1998, Blumenschine 1995). However, Domínguez-Rodrigo and Barba (2006) argued that this high frequency of tooth marks on the FLK *Zinjanthropus* faunal was overestimated due to the equifinality of natural biochemical marks. Domínguez-Rodrigo and Barba's (2006) reanalysis of FLK *Zinjanthropu*s archaeofauna yielded a relatively low incidence (11%) of carnivore toothmarks, purporting that the assemblage has been affected by biochemical marks. Consequently, they used this criterion as a justification to falsify the C-H-C hypothesis.

However, falsification of the C-H-C model was largely based on unjustifiable reasons. For example, Domínguez-Rodrigo and Barba (2006) do not provide details of the protocol or methods used to establish the experimental/referential framework for their “biochemical marks”, hitherto known as bio-erosion in archaeological and palaeontological research (Neuman 1966; Blumenschine *et al.*, 2006). As a result, Domínguez-Rodrigo and Barba's (2006) study cannot be replicated for testing their hypothesis of the formation of biochemical marks. Conversely, Blumenschine's (1986, 1987,1995) studies on the protocol for identifying passive scavenging have been independently tested and replicated with other studies (e.g., Selvaggio 1994a, b, 1998; Lupo 1995; Capaldo 1995, 1997).

Another criterion used by Domínguez-Rodrigo*et al.,* (2014: 33) for hominins having primary access to the flesh of carcasses is the high incidence of cut marks on the FLK *Zinjanthropus* assemblage. Nonetheless, hominin-induced butchery marks particularly cut marks on fauna remains vary considerably (Domínguez-Rodrigo2009; Merritt 2012; Pobiner *et al.*, 2018; Badenhorst and Kimambo 2021). Various factors contribute to this including the type of raw material used for butchery (Greenfield 2006; de Juana *et al.*, 2010 Merritt 2012), carcass size (Lyman 1987, 1992; Marshall 1986; Gifford-Gonzalez 1989) experience of the butcher/ butcher skills (Hynes 1993; Lyman 1995; Domínguez-Rodrigo 1997, 2002; Lupo 2012; Haynes and Krasinski 2010), bone fragmentation (White 1952),analytical biases (Abe *et al.,* 2002; Domínguez-Rodrigo *et al.,* 2009; Pante *et al.,* 2015) crocodile tooth mark that mimic cut marks can potentially increase the number of cut marks (Sahle *et al.*, 2017; Domínguez-Rodrigo and Baquedano 2018), postmortem carcass condition (Binford 1981, 1984, 1988), animal trampling (Behrensmeyer *et al.*, 1986; Pineda *et al.*,2019), as well as the amount of flesh available in the carcasses (Bunn 1982, 2001; Bunn and Kroll 1986; Binford 1986; Blumenschine 1988, 1995; Selvaggio 1994a, 1998; Domínguez-Rodrigo 1997; Pobiner and Braun 2005; Domínguez-Rodrigo *et al.,* 2009; Pante *et al.*,2012).

Traditionally, the timing for hominin and carnivore access to carcass is based on the incidence of cut marks (Bunn 1981, Domínguez-Rodrigo1997, 2009). However, the interpretation of cut marks on faunal remains has produced conflicting results. For example, the high incidence of cut marks on mid-shaft portions is used as justification for FLK Zi*njanthropus* hominins having primary access to fleshed carcasses (Bunn 1981,1982,1983, Bunn and Kroll 1986; Domínguez-Rodrigo1997, 2009; Domínguez-Rodrigo*et al.,* 2014). Further, using the evidence of cut marks, Bunn and Kroll (1986) have argued that hominins at the site were systematically butchering the carcass. This implies that the systematic butchering was completed by at least an experienced or expert butcher who is familiar with the anatomy of a carcass. If this is the case, the incidence of butchery marks would be the opposite of Bunn’s (1981) and Domínguez-Rodrigo's (1997) results. Several researchers have shown that an experienced butcher leaves few cut marks on the animal bone (Lyman 1995: 237; Domínguez-Rodrigo 1997; Pobiner *et al.*, 2018). For instance, Domínguez-Rodrigo (1997) demonstrates that the decrease in the frequency of cut marks in his experiments was relative to the increase in his butchery experience. Therefore, this suggests that a high number of cutmarks on the fossil remains can be due to other factors such as butchery experience, butchery style, and the type of tools used. Braun *et al.*, (2016) add that the mechanical property of stone tools and physical property of the bone cause variability of butchery marks on bones. As such, cut marks on faunal remains may not necessarily be associated with the amount of flesh on the carcass (Stiner *et al.*, 1995, 201; Merritt 2012; Braun *et al.*, 2016; Pobiner *et al.*, 2018).

Moreover, various researchers have documented modifications that resemble cutmarks. For instance, Sahle *et al*., (2017) have shown that crocodile tooth marks on animal bones generate grooves that are very difficult to distinguish from hominin-induced cut marks. Carnivore furrowing can mimic cut and chop marks generated by stone tools or metal blades (Haynes 1983). According to Pineda *et al.*, (2019), trampling on dry bones leaves modifications that mimic butchery marks. If not properly identified, these factors can equally all create marks that look like cut marks. Therefore, cut mark data alone is not enough to determine hominins' primary or secondary access to carcasses. For this reason, scholars (e.g., Blumenschine 1988, 1995, Selvaggio 1994, 1998) recommended the use of percussion and carnivore tooth marks. Pante *et al.*, (2012, 2015) recommended that both cut, percussion, and carnivore modification marks should be used simultaneously to generate a meaningful interpretation of primary or secondary access to carcasses by hominins.

Domínguez-Rodrigo*et al.,* (2014: 34) have also criticised the general name for the C-H-C model because the data of Blumenschine (1988, 1995) involved actualistic studies of humans and hyena bone modification. They consider Domínguez-Rodrigo´s (1997) data as accurate for the C-H-C model with a slight modification. Domínguez-Rodrigo*et al.,* (2014) suggested that such a model should be regarded as Felids-Hominin-Hyena (F-H-H) since other multiple carnivores feed on the carcasses, but their feeding sequence data are lacking. This observation seems to be reasonable. However, Domínguez-Rodrigo's (1997) data cannot be replicated because it lacks a controlled experiment (Blumenschine 1988, 1995). For instance, observation of carnivore feeding behaviour in Domínguez-Rodrigo (1997a) study did not follow the complete process of lion carcass consumption.

Various studies have documented the patterns of felid carcass consumption and the characteristic of their food disposal (Haynes 1983, Pobiner 2015). In most cases, multiple carnivores consume a single carcass, such as lions followed by other carnivores such as hyenas and jackals (Brain 1981; Blumenschine 1987, 1988; Selvaggio 1994; Pobiner and Blumenschine 2003). Pobiner and Blumenschine (2003) stressed that different families, genera, and species of mammalian carnivores have unique and selective feeding behaviour on a carcass of the same size (also see Haynes 1983). Carnivore feeding on a carcass leaves modification marks in the form of pits, scores, tooth notches, furrows, gnaws, and puncture marks (Haynes 1980; Blumenschine 1988; Selvaggio 1994; Gidna 2014). These help to establish which carnivores fed on the carcasses (Haynes 1983; Selvaggio 1994; Pobiner and Blumenschine 2003). Blumenschine (1986,1988,1995) has repeatedly offered a detailed explanation of the possible hominin scavenging niches, including de-fleshed carcasses from lion kills, hominins scavenging carcasses of animals derived from natural death or drowns, as well as fleshed medium-sized bovids from leopard-stored kills (Blumenschine 1986, 1987, 1988, 1995; Cavallo and Blumenschine 1989, Blumenschine and Cavallo 1991).

Blumenschine and Cavallo (1991: 94) have also hypothesised that large carcasses with a considerable amount of flesh could have been obtained from saber-toothed cats. Nonetheless, Domínguez-Rodrigo (1997, 1999, 2002), Domínguez-Rodrigo, *et al*, (2014 and reference therein) have consistently focused on the C-H-C model but avoided other proposed scavenging opportunities which address the critical issues on the variability of carnivore and hominin induced surface modification on faunal assemblages.

2.4.2 Carnivore Only (CO)

The C-O model is characterised by an assemblage that has been consumed by single or multiple carnivores only with the fragmentation completed with hyenas (Blumenschine 1988, 1995; Capaldo 1998a, b; Pante 2010). Experimental material used to mold this model included major long bones found in bovids of different sizes (details in Blumenschine 1988, 1995). The diagnostic feature of the assemblage generated from C-O is the presence of a carnivore-induced mark only. When the carcasses are fed and accumulated by hyenas as a primary consumer, the assemblages consist of tooth-marked long bone fragments with a frequency of over 67% with an average of approximately 82%.

2.4.3 Hammerstone-to-Carnivore (H-C)

The hammerstone-to-carnivore model (Blumenschine 1988, 1995) represents a sequence where hominins are responsible for processing carcasses to collect the majority of resources (flesh and marrow) but excluding grease (also see Capaldo 1995, 1998b; Pante *et al.*, 2012). The experimental process for this model was completed by skinning, dismembering, disarticulation, de-fleshing, and periosteum removal using a metal blade. Then hammerstones and anvils were used to break long bones to access bone marrow. Subsequently, the long bone samples were discarded in open *Acacia* woodlands and fed upon by scavenging hyenas. The key features of H-C assemblages are the absence of epiphyseal fragments, the highest frequency of tooth-marked long bone fragments (about 45%, with an average of approximately 15%), and a relatively low number of tooth-marked shaft fragments (Blumenschine 1988; 1995).

2.4.4 Hammerstone Only (HO)

This model represents a sequence where carnivores have all access to flesh on a carcass but leaves long bone with marrow intact. In this case, marrow is the only resource left for scavenging hominins. Thus, hominins break long bones to access the marrow resulting in a high incidence of percussion marks compared to cut marks in the assemblage (Selvaggio 1994). Furthermore, the mean incidence of percussion marks in the HO model is higher than H-C and V-H-C models. However, according to Pante *et al.*, (2012), this observation is not compatible with mammal group size 1 and 2 mid-shaft fragments from fossil records because the H-C model has the highest mean incidence of percussion-marked specimens (Pante *et al.*, 2012: 398).

2.4.5 Whole Bone-to-Carnivore (WB-C)

The Whole Bone-to-Carnivore model describes the sequence where hominins process whole carcasses for abdominal contents and flesh, and carnivores consume grease and marrow (Capaldo 1998: 314). The experimental data for this model was completed by dismembering and complete removal of the flesh from a carcass using a metal knife (Capaldo 1995, 1998). Most of the elements were not disarticulated. The skin on the long bones was neither removed nor scraped and the periosteum was left intact. The bone elements were discarded for secondary scavengers. Jackals, storks, and hyenas were the second consumers of the bones. However, while jackals and storks caused a minimal impact on the assemblage, hyenas are the only scavengers that had a substantial impact on the bone. According to Capaldo (1995, 1998), a key feature of the WB-C model is the near-complete deletion of long-bone epiphyses by hyenas. Furthermore, long bones lack percussion marks, and the distal ends are large than those produced by hammerstone marks.

2.5 Chapter Summary

This chapter has provided an overview of the taphonomic traces on fauna remains. Given that bone surface modifications from different agents can mimic each other, understanding their taphonomic signatures are of paramount importance. This helps to avoid any misinterpretation of faunal assemblages from archaeological sites. This chapter has also reviewed the hunting *vs.* scavenging behaviour of early hominins. Hunting or scavenging behaviour defines who has primary or secondary access to a carcass. Indeed, this is not easy to deduce without an understanding of the feeding sequence of carnivores and their resulting features on a carcass. Accordingly, models derived from ethological and taphonomic studies have helped to detect primary and secondary access of a carcass from the fossil remains. The HWK EE faunal exhibits rich and complex feeding traces left by hominins and carnivores. Thus, the taphonomic and various feeding models presented in this chapter will help to interpret the feeding behaviour of late *Homo habilis* at HWK EE.

Chapter Three

3 Material and Methods

3.1 Introduction

The HWK EE fauna remains used in this study are curated at the Olduvai Gorge Archaeology Project (OGAP) laboratory in Olduvai Gorge, northern Tanzania. All the analysis was completed at the OGAP laboratory. Access to use the HWK EE data was granted by the OGAP directors, and all published and unpublished data used herein was provided by Prof. Michael Pante of Colorado State University, USA. The HWK EE fauna sample comprises over 29000 fauna remains (Pante and de la Torre 2018, Pante *et al.,* 2018). These remains were retrieved from four different archaeological trenches [Trench 1-Main Trench, T27, T28, and T29: Plate 1] (de la Torre *et al.,* 2018a; Pante et al., 2018, Pante and de la Torre 2008). The archaeological material from these trenches was excavated from three stratigraphic intervals (Lower Augitic Sandstone [LAS], LEMUTA, and Tuff IIB). However, only two stratigraphic intervals (LEMUTA and LAS) yielded most of the fauna remains recovered from the site. These two intervals are associated with Oldowan technology (de la Torre *et al.,* 2018a). Thanks to the meticulous excavation technique carried out by OGAP all large specimens were left insitu for mapping using a total station, conservation (where needed), and carefully packed with their respective contextual information. All specimens measuring less than two centimeters were retrieved during screening (see details in de la Torre *et al.,* 2018a, Pante *et al.,* 2018).

The taphonomic analysis of this study is built on Pante *et al.'s,* (2018) study of butchery and carnivore modification marks for the assemblage. Pante *et al.,* (2018) completed analyses on the HWK EE sample including the identification of specimens (NISP) to taxa-level and animal size class (following the Bunn 1982), calculating the minimum number of elements (MNE), and recording weathering, butchering marks, and breakage patterns (see Pante *et al.,* 2018 for more details). The majority of these aspects will not be reproduced in this study. Instead, some aspects will be adapted from HWK EE data provided by Prof. Michael Pante to address the research questions raised in this study. The current study focuses on hominins butchery and carnivore modification marks only. Hominin butchery and carnivore-induced modification marks, a subject of this study, are the direct evidence used to establish the order of hominin and carnivore access to a carcass.

3.2 Animal Size Class

The initial description of HWK EE mammal size class in Pante *et al.*, (2018) was described following criteria outlined in Brain (1974, 1981: 9), Bunn (1982), and Blumenschine (1986). In these studies, the sizes of mammals were classified from mammal size class 1 to 6 depending on the comparison of the adult live weight of an animal. For instance, the adult mammals' size class 1 live weight is <50lb. This group includes mammals such as Thomson's gazelle. Grant's gazelle and impala are mammals in the size 2 class and weigh between 50-250lbs. Wildebeest and zebra are grouped into mammal size class 3, weighing between 250 and 750lbs. Mammals weighing between 750-2000lbs are classified into the mammal size 4 groups. Any mammals weighing 2000-6000 lbs., including giraffes, hippos, and rhinos, are classified as mammal size class 5whilesize 6 (elephants only) are over 6000 lbs.

The analysis of butchery and carnivore-induced marks per animal and skeletal part in this study follows criteria published in Domínguez-Rodrigo (2009) from the BK site. However, Domínguez-Rodrigo (2009). lumped mammal size 3 within the group of larger mammals size 4 and above. The author did so because long bones for large mammals beyond size 3 were few. This study maintains Domínguez-Rodrigo's (2009) criteria for classifying small mammals.

Elsewhere, Blumenschine (1986) considers mammals size class 3 as a medium-sized mammal, and mammals' sizes 4 and above are described as larger mammals size class. The current study uses the description method of Blumenschine's (1986, 1988) for medium and large mammals.

3.3 Skeletal Elements

HWK EE long bone elements used in this study were initially divided into five portions following a system used by Blumenschine (1988, 1995). These portions include proximal epiphyses (PEPI) and distal epiphyses (DEPI) which are bounded by the metaphysis and include articular and non-articular bone. The proximal near-epiphysis (PNEF) and distal near-epiphyses (DNEF) of long bones extend from the metaphysis to the beginning of the midshaft cross-section and include muscle attachments like the deltoid and radial tuberosities, lesser trochanter, and tibial crest. These features also have cancellous medullary surfaces. Midshaft (MSH) portions occur between PNEF and DNEF portions and have smooth medullary surfaces (Pante *et al.*, 2018: 218). However, long bone elements in this study are analysed following the system used by Domínguez-Rodrigo (1997, 2009). The latter system was used because according to by Domínguez-Rodrigo (1997) Domínguez-Rodrigo *et al.,* (2009) count of butchery marks based on the near-epiphysial portion is subjective. Domínguez-Rodrigo *et al.,* (2009: 266) claim that a specimen measuring 10 cm of trabecular tissue on its medullary surface may be classified as a near-epiphysial portion even though marks occur on the midshaft portion that makes up 90% of the specimen. Therefore, the long bone elements in this study were divided into three sections, namely proximal ends, shafts, and distal ends. To achieve this, the data from HWKEE for long bone elements (Pante *et al.,* 2018: 218).) were transformed into the following format: PEPI was considered as a proximal end, PNEF, MSH, and DNEF were tallied as MSH, and DEPI were considered as distal ends.

3.4 Taphonomy

Traces of cut and percussion marks as well as tooth marks were examined macroscopically using a 60w table lamp followed by closer inspection with a 10X hand lens. Identified marks were further examined using a portable Dino-lite microscope at magnifications of up to 60 (Pante *et al.,* 2018: 218). The induced modification marks were tallied by the presence or absence of marks based on taxon, mammal size, skeletal element, and the location of the marks per element, taxon, and mammal size. Induced modification marks were photographed with a portable microscope and/or a Nikon D7100 camera equipped with a 40 mm macro lens and Helicon focus (Pante *et al.,* 2018: 218). The definition of a cut mark as used in this study follows the morphological criteria outlined in Bunn (1981) and Potts and Shipman (1981). Potts and Shipman (1981:577) describe cut marks as "elongated grooves with V-shaped cross-sections (and) many, fine parallel striations ... within each main groove". Cutmarks are differentiated from tooth or trampling marks by the presence of microstriations within the groove, and by the groove itself being more V-shaped than other marks (Bunn, 1982; Bunn and Kroll 1986).

In this study, the tally for cutmarks on the long bone elements is based on criteria outlined in Domínguez-Rodrigo (1977a, b) and Domínguez-Rodrigo *et al.*, (2009) with slight modifications. The reasons for this are as follows. Domínguez-Rodrigo (2009) divided long bone elements into three sections: proximal ends, midshafts, and distal ends. However, the tally for complete bones was not provided. It is possible that complete elements were missing from the analysis. Opposingly, the HWK EE sample contains some complete skeletal elements with traces of cut marks. For this reason, the current study divided the long bones into four categories: complete, proximal ends, midshafts, and distal ends, to ensure a correct tally of cut marks on the respective element sections. It should be noted that all induced modifications on long bone were recorded based on their location per bone section such as proximal, midshaft and distal end. Presence of complete long bone with butchery marks is an indication that hominins exploited flesh but not bone marrow from the carcass (Pante *et al.*, 2018).

Percussion marks (PM) were principally described by following criteria outlined by Blumenschine and Selvaggio (1988) and Blumenschine (1995). Blumenschine and Selvaggio (1988) described PM as hominin-induced marks comprised of pits, grooves, and striae, which may or may not be associated with notches. PMs are generally characterised by dense-packed and parallel microstriations within or close to the pits or grooves, or alternatively, may be found in lieu of a pit or groove. These kinds of microstriations are unique features that differentiate hominin PM from other actors e.g., microstriations resulting from carnivore gnawing (Blumenschine and Selvaggio 1988; Blumenschine 1995).

Tooth marks were identified by considering the criteria outlined in Blumenschine (1995) and Binford (1981:44-49). According to Binford (1981), carnivore tooth marks on the bone surfaces produce punctures, furrows, pits, and scores. Blumenschine (1995:29) notes that pits and scores are commonly identified as bowl-shaped or angular indentations resultant of static loading from the carnivore's tooth on the surface of the bone, and scores by grooves that are u-shaped and typically lack microstriations. Crocodiles produce V-shaped marks which resemble cutmarks. However, crocodile tooth marks contain continuous internal microstriation. The striae are symmetrically located on one side of the groove, with a small number of striations and great separation in between them. In contrast, cut marks made by stone tools contain a greater number of tightly packed microstriations on both sides of the groove (Domínguez-Rodrigo and Baquedano 2018). Contrary to the initial analysis of butchery and carnivore marks on long bone elements only (Pante *et al.*, 2018), the current study uses a range of all skeletal elements recovered at HWK EE to assess the order of hominin and carnivore feeding behavior at the site. The frequency of tooth marks was counted by a simple count of the presence or absence of marks on the skeletal element. Traces of butchery, carnivore, and crocodile marks were quantified into percentages based on animal size class, skeletal elements, and portion. These percentages are used to infer hominin-carnivory behaviour at the site.

CHAPTER FOUR

4 RESULTS

4.1 The HWK EE Assemblage

The total sample from HWK EE reported in Pante *et al.,* (2018) encompasses over 29,000 specimens (Table 1), representing different taxa, animal sizes, and skeletal elements. Detailed analyses of these aspects are reported elsewhere (see: Pante and de la Torre 2018; Pante *et al.,* 2018). The current study focuses on the fauna sample recovered from the LAS and LEMUTA intervals (Table 1) which contain 4493 bones. The NISP fauna recovered from TUFF IIB are relatively few (Pante *et al.,* 2018) and these are not included in this study. Fauna from LAS and LEMUTA intervals encompasses both micro-and macrofaunae remains. For this study, microfauna is excluded in the analysis of butchery (i.e., cut and percussion marks) and the analysis of land carnivore and crocodile-induced marks. This restriction is based on the simple reason that hominins feeding models focusing on primary and secondary access to carcasses by hominins are based on mammals' size 1and above (e.g., Blumenschine 1995; Pante *et al.,* 2018). Smaller mammals below size 1 may have been hunted and consumed by hominins, but they do not offer any potential information regarding carnivore and hominins interactions or the exploitation of marrow.

Table 1: The HWK EE Assemblage

Interval	**NISP Bones**	**NISP Teeth**	**Unidentified Specimens (Indet)**	**Total**	**Percentage**
LAS	2614	486	21 319	**24419**	**84**
LEMUTA	1847	308	1981	**4136**	**14**
TUFF IIB	32	34	491	**560**	**2**
Total	**4493**	**828**	**23791**	**29115**	**100**
Percentage	**15**	**3**	**81**		

Pante *et al.,* (2018) reported the presence of various taxa found in the HWK EE fauna assemblage. However, the authors did not provide the count of each taxon found in the sample. Table 2 below provides a NISP count of taxa recorded from the HWKEE sample. Most of the fauna remains (3548, 79%) could not be assigned to any taxon. Of the remaining fauna, Bovidae are the most dominant (818, 18%) in the sample. Equidae and microfauna are presented with one percent each. The remaining taxa, Proboscidea, Rodentia, Carnivora, Rhinocerotidae, Suidae, Hippotamidae, Giraffidae, and Reptilia are also present in the sample but in minimal numbers with less than one percent each. The frequency of taxa per interval shows that the LAS interval has a higher number for most taxa (Bovidae, Giraffidae, Equidae, primate, Carnivora, and microfauna) than the LEMUTA interval. The frequency of Reptilia and Suidae are even in both

LAS and LEMUTA intervals. Rodentia and Hippotamidae were recorded in the LAS interval only.

Table 2: NISP Count of Taxa in the HWK EE Sample

Taxa	**Interval**		**Total**	**Percentage**
	LAS	**LEMUTA**		
Proboscidea	3	2	**5**	**<1**
Rodentia	2	0	**2**	**<1**
primate	4	2	**6**	**<1**
Carnivora	12	2	**14**	**<1**
Rhinocerotidae	2	1	**3**	**<1**
Equidae	29	18	**47**	**1**
Suidae	8	8	**16**	**<1**
Hippotamidae	2	0	**2**	**<1**
Giraffidae	8	2	**10**	**<1**
Bovidae	485	333	**818**	**18**
Reptilia	2	2	**4**	**<1**
Microfauna	12	5	**17**	**1**

Indet	2066	1482	**3548**	**79**
Total	**2635**	**1858**	**4493**	**100**
Percentage	**59**	**41**		

The NISP count of skeletal elements in the LAS and LEMUTA interval (Table 3) is dominated by long bone midshaft elements (24%) and ribs (9%). Percentages of cranium, humeri, tibiae, and phalanges in the sample are even (3% each). Other skeletal elements showing similar patterns include mandibles, thoracic vertebrae, pelvises, scapulae, metacarpi, femora, metatarsi, metapodia, carpals, and tarsals (2% each) as well as horncores, maxillae, vertebrae (cervical, lumbar), and ulnae (1% each). The remaining skeletal elements are represented by less than one percent each. Apart from metacarpi, ribs, pelvises, and vertebrae, most of the elements in the sample occur in higher frequencies in the LAS than in the LEMUTA interval.

Table 3: NISP Count of Skeletal Element in LAS and LEMUTA Interval

Element	**LAS**		**LEMUTA**		**Total**	**Percentage**
	Count	**Percentage**	**Count**	**Percentage**		
Horncores	38	1	17	1	**55**	**1**
Cranium	66	3	84	5	**150**	**3**
Maxillae	18	1	8	<1	**26**	**1**

Mandibles	40	2	27	2	**67**	**2**
Atlases	5	<1	3	<1	**8**	**<1**
Axis	3	<1	2	<1	**5**	**<1**
Cervical vertebrae	21	1	23	1	**44**	**1**
Thoracic vertebrae	47	2	25	1	**72**	**2**
Lumbar vertebrae	27	1	15	1	**42**	**1**
Caudal	7	<1	3	<1	**10**	**<1**
Sacral vertebrae	8	<1	5	<1	**13**	**<1**
Vertebrae indet	21	1	27	2	**48**	**1**
Pelvises	35	1	40	2	**75**	**2**
Scapulae	57	2	47	3	**104**	**2**
Ribs	181	7	233	13	**414**	**9**
Humeri	55	2	62	3	**117**	**3**
Radii and Ulnae	2	<1	3	<1	**5**	**<1**
Radii	46	2	57	3	**103**	**2**
Ulnae	20	1	21	1	**41**	**1**

Metacarpi	44	2	50	3	**94**	**2**
Femora	45	2	45	2	**90**	**2**
Tibiae	73	3	66	4	**139**	**3**
Fibulae	7	<1	1	<1	**8**	**<1**
Metatarsi	50	2	49	3	**99**	**2**
Metapodia	52	2	27	2	**79**	**2**
Carpals/Tarsals	65	2	14	1	**79**	**2**
Astragalus	15	1	7	<1	**22**	**<1**
Calcanea	11	<1	1	<1	**12**	**<1**
Navicular bones	9	<1	2	<1	**11**	**<1**
Phalanges	96	4	20	1	**116**	**3**
LBN /MSH	600	23	463	25	**1063**	**24**
NID	867	33	407	22	**1274**	**28**
Others	4	<1	4	<1	**8**	**<1**
Total	**2635**	**100**	**1858**	**100**	**4493**	**100**

4.2 Length of Bone Elements

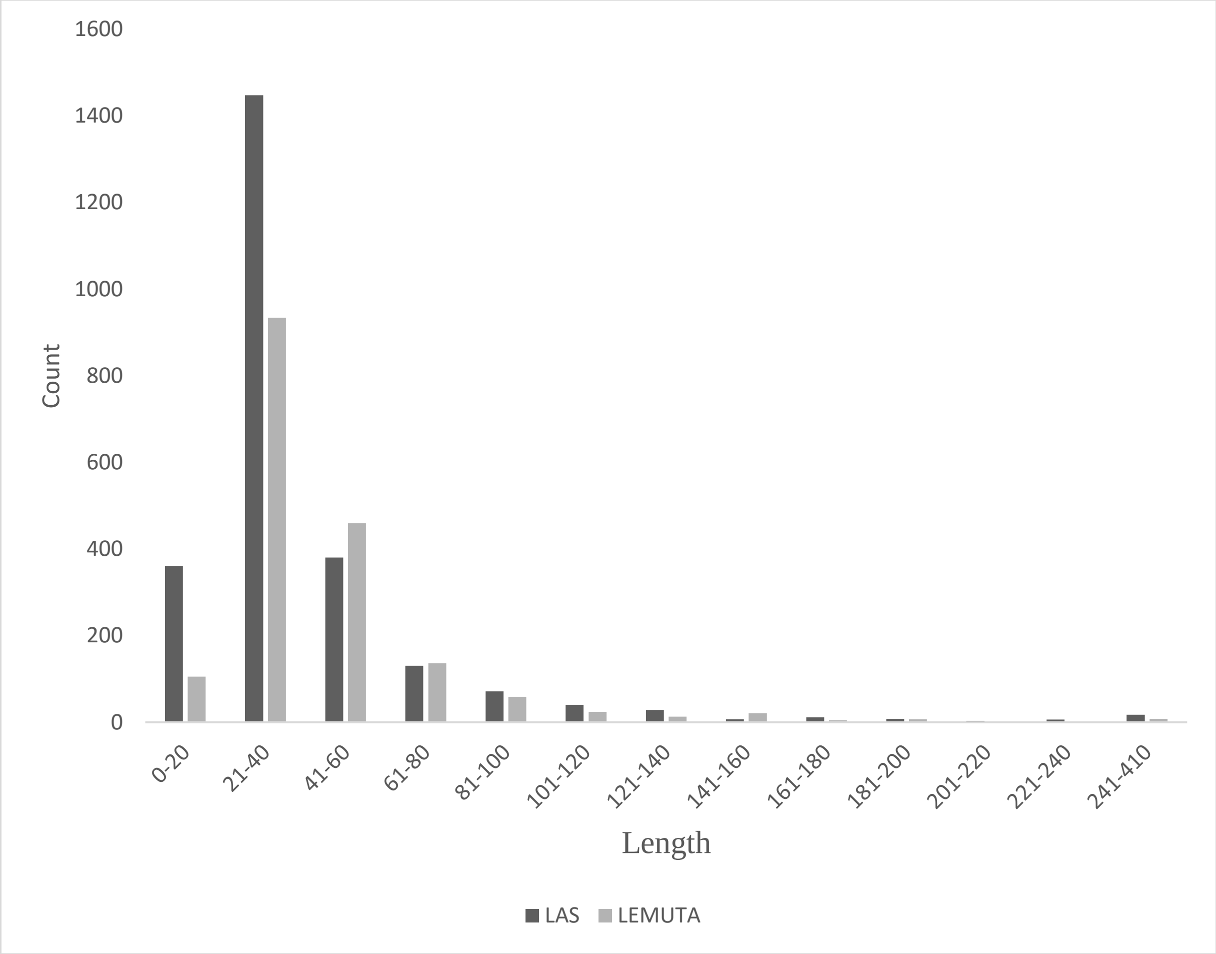
The sample is heavily fragmented, with most specimens having a length of 2-4 (56%) and 4-6 cm (20%) (Table 4: Figure3). Few complete elements are present in the sample. The frequency of the fragmented sample indicated below is less than the original sample presented earlier because some elements (e.g., horncores, horns) were not included.

Table 4: Length (mm) of Skeletal Elements in the LAS and LEMUTA Interval

Length (mm)	LAS	LEMUTA	Total	Percentage
0-20	361	105	466	**11**
21-40	1447	934	2381	**56**
41-60	380	459	839	**20**
61-80	130	136	266	**6**
81-100	71	59	130	**3**
101-120	40	24	64	**1**
121-140	28	13	41	**1**
141-160	7	21	28	**1**
161-180	11	5	16	**<1**
181-200	8	7	15	**<1**
201-220	3	1	4	**<1**

221-240	6	1	7	**<1**
>241	17	8	25	**1**
Total	**2509**	**1773**	**4282**	**100**
Percentage	**59**	**41**		

Figure 3: Length of all Skeletal Element in LAS and LEMUTA Interval



4.3 Mammal Sizes

Considering mammal size class, a total number of 3221 (46%) specimens (Table 5) represents small (mammal size class 1 and 2), medium (mammal size class 3), and large mammals (mammal size class 4, 5, and 6). The remaining sample (n=1272, 28%) are fauna smaller than mammal size class 1. Overall, over half (2134, 64%) of the sample is comprised of small mammals. This is followed by medium-sized mammals (n=974, 29%). Large-sized mammals are present but only in a minimal percentage (n=111, 3%). Considering mammal size representation per interval, small to large size mammals occur in a higher number in the LAS (53%) than in the LEMUTA interval (43%). Nonetheless, mammal size representation is consistent in both intervals. That is, in both LAS and LEMUTA intervals, small mammals dominate the sample, followed by medium and large mammal sizes.

Table 5: NISP Count of Mammal Size in the HWK EE Sample

Animal Size	**LAS**	**LEMUTA**	**Total**	**Percentage**
Small (1,2)	1171	963	**2134**	**46**
Medium (Size 3)	527	447	**974**	**21**
Large (4,5,6)	67	44	**111**	**2**
Indet		2	**2**	**<1**
NID	870	402	**1272**	**28**
Total	**2635**	**1858**	**4493**	**100**
Percentage	**53**	**47**		

The LAS interval produced over 2600 elements (Table 6). Of these, 867 (33%) remains could not be assigned to a specific skeletal element or mammal size. The remaining sample represents all skeletal elements. The count of mammal sizes in the LAS interval revealed that small mammals are most dominant (n=1169, 44%). Medium-sized mammals are represented by 507 (19%) elements. Large mammals occur in a lower frequency (n=66, 3%).

The NISP count of all sections on all long bone elements produced the following results. Small mammal long bone elements are dominated by midshafts sections (n=576, 49%). The frequency of proximal and distal ends produced nearly the same results (n=46, 4 % and n=40, 3% respectively). Overall, less than one percent of the complete long bone elements were recorded for small mammals. The patterns of the long bone section representation for medium-sized mammals are consistent with small mammals. That is, midshafts of medium-sized mammals are higher (n=184, 19%), with the proximal and distal sections of long bones being even (n=38, 4% each) while complete elements are rare (n=6, 1%). Like the previous results of the long bone sections in small and medium mammals, the midshaft section (n=19, 59%) is dominant for the large mammals followed by the distal section (n=7, 23%) and proximal section (n=6, 19%).

Table 6: NISP Count of Mammal Sizes per Skeletal Elements in LAS Interval

Element	**Section**	**Animal Size**				**Total**	**Percentage**
		Small	**Medium**	**Large**	**Indet**		
Horns		26	11	0	1	**38**	**1**

Cranium		44	21	0	1	**66**	**3**
Maxillae		10	7	1	0	**18**	**1**
Mandibles		26	12	2	0	**40**	**2**
Atlases		2	2	1	0	**5**	**<1**
Axis		1	2	0	0	**3**	**<1**
Cervical vertebrae		9	11	1	0	**21**	**1**
Thoracic vertebrae		32	14	1	0	**47**	**2**
Lumbar vertebrae		21	5	1	0	**27**	**1**
Caudal		6	1	0	0	**7**	**<1**
Sacral vertebrae		7	1	0	0	**8**	**<1**
Vertebrae indet		20	1	0	0	**21**	**1**
Pelvises		22	9	4	0	**35**	**1**
Scapulae		40	16	1	0	**57**	**2**
Ribs		109	58	13	1	**181**	**7**

Humeri	Complete	1	0	0	0	**1**	**<1**
	Proximal end	4	1	1	0	**6**	**<1**
	Midshaft	21	8	0	0	**29**	**1**
	Distal end	12	6	1	0	**19**	**1**
	Indet/other	0	0	0	0	**0**	**0**
Radii and Ulnae	Complete	0	0	0	0	**0**	**0**
	Proximal end	0	0	0	0	**0**	**0**
	Midshaft	1	0	0	0	**1**	**<1**
	Distal end	0	0	0	0	**0**	**0**
	Indet	0	1	0	0	**1**	**<1**
Radii	Complete	1	1	0	0	**2**	**<1**
	Proximal end	5	11	1	0	**17**	**1**
	Midshaft	14	6	1	0	**21**	**1**
	Distal end	3	3	0	0	**6**	**<1**
	Indet	0	0	0	0	**0**	**0**

Ulnae	Complete	0	0	0	0	**0**	**0**
	Proximal end	6	4	1	0	**11**	**<1**
	Midshaft	7	0	0	0	**7**	**<1**
	Distal end	0	0	0	0	**0**	**0**
	Indet/other	0	0	0	2	**2**	**<1**
Metacarpi	Complete	0	0	0	0	**0**	**0**
	Proximal end	7	7	1	0	**15**	**1**
	Midshaft	11	10	2	0	**23**	**1**
	Distal end	1	3	0	0	**4**	**<1**
	Indet	2	0	0	0	**2**	**<1**
Femora	Complete	0	0	0	0	**0**	**0**
	Proximal end	3	1	0	0	**4**	**<1**
	Midshaft	15	15	0	0	**30**	**1**
	Distal end	5	5	1	0	**11**	**<1**
Tibiae	Complete	0	1	0	0	**1**	**<1**

	Proximal end	6	4	1	0	**11**	**<1**
	Midshaft	30	12	4	1	**47**	**2**
	Distal end	5	6	3	0	**14**	**1**
Fibulae	Complete	3	1	0	0	**4**	**<1**
	Proximal end	0	0	0	0	**0**	**0**
	Midshaft	0	3	0	0	**3**	**<1**
	Distal end	0	0	0	0	**0**	**0**
Metatarsi	Complete	0	2	0	0	**2**	**<1**
	Proximal end	11	9	0	0	**20**	**1**
	Midshaft	20	2	3	0	**25**	**1**
	Distal end	1	1	1	0	**3**	**<1**
Metapodia	Complete	0	1	0	0	**1**	**<1**
	Proximal end	4	1	0	0	**5**	**<1**
	Midshaft	12	4	0	2	**18**	**1**
	Distal end	13	14	1	0	**28**	**1**

Carpals/Tarsals		31	31	3	0	**65**	**2**
Astragalus		10	3	2	0	**15**	**1**
Calcanea		7	3	1	0	**11**	**<1**
Navicular bones		5	4	0	0	**9**	**<1**
Phalanges		52	42	1	1	**96**	**4**
LBN/Midshaft		463	124	13	0	**600**	**23**
NID		2	0	0	865	**867**	**34**
Others					4	**4**	**<1**
Total		**1169**	**521**	**67**	**878**	**2635**	**100**
Percentage		**44**	**19**	**3**	**33**		

The patterns of skeletal element representation per animal size in the LEMUTA interval are consistent with the LAS interval (Table 7). Small mammals occur in high frequencies (n=958, 52%) followed by medium-sized mammals (n=449, 22%), and few (n=43, 2%) large mammals. Regarding skeletal elements, the LEMUTA interval is dominated by midshaft bones (25%), ribs (13%), and craniums (5%), while the remaining skeletal elements occur in lesser numbers. The count of all long bone sections per animal size revealed the following results. Small mammals have the highest number of midshaft sections (n=532, 55 %). The difference between proximal and distal sections for all long bones of small mammals is minimal (n=27, 3%*vs* n=26, 3%). Only 10 (1%) complete elements were recorded for small mammals. Like small mammals, the long bone sections for medium-sized mammals in the LEMUTA interval are dominated by midshafts (n=189,42%). The distal sections are slightly more numerous (n=21) than the proximal sections (n=18). Only five complete elements were recovered for medium-sized mammals. The proximal sections for large mammals are represented by five midshafts and two distal sections only.

Table 7: NISP Count of Mammal Size per Skeletal Element in LEMUTA Interval

Element		**Animal size**				**Total**	**Percentage**
		Small	**Medium**	**Large**	**Indet**		
Horns		13	3	1	0	**17**	**1**
Cranium		62	22	0	0	**84**	**5**
Maxillae		5	3	0	0	**8**	**<1**
Mandibles		17	9	1		**27**	**1**
Atlases		2	1	0	0	**3**	**<1**
Axis		1	1	0	0	**2**	**<1**
Cervical vertebrae		4	18	1	0	**23**	**1**

Thoracic vertebrae		13	12	0	0	**25**	**1**
Lumbar vertebrae		11	4	0	0	**15**	**1**
Caudal		2	1	0	0	**3**	**<1**
Sacral vertebrae		1	3	1	0	**5**	**<1**
Vertebrae indet		21	6	0	0	**27**	**1**
Pelvises		13	26	1	0	**40**	**2**
Scapulae		27	18	2	0	**47**	**3**
Ribs		137	74	22	0	**233**	**13**
Humeri	Complete	1	1	0	0	**2**	**<1**
	Proximal end	0	0	1	0	**1**	**<1**
	Midshaft	27	15	1	0	**43**	**2**
	Distal end	9	6	1	0	**16**	**<1**
	Indet/Othe	0	0	0	1	**1**	**<1**

	r						
Radii and Ulnae	Complete	1	0	0	0	**1**	**<1**
	Proximal end	0	1	0	0	**1**	**<1**
	Midshaft	0	1	0	0	**1**	**<1**
	Distal end	0	0	0	0	**0**	**0**
Radii	Complete	4	0	0	0	**4**	**<1**
	Proximal end	3	6	0	0	**9**	**<1**
	Midshaft	29	13	1	0	**43**	**2**
	Distal end	0	0	0	0	**0**	**0**
	Indet	1	0	0	0	**1**	**<1**
Ulnae	Complete	0	0	0	0	**0**	**0**
	Proximal end	3	2	0	0	**5**	**<1**
	Midshaft	8	7	0	0	**15**	**<1**
	Distal end	0	1	0	0	**1**	**<1**

Metacarpi	Complete	1	1	0	0	**2**	**<1**
	Proximal end	5	1	0	0	**6**	**<1**
	Midshaft	20	12	1	0	**33**	**2**
	Distal end	3	5	0	0	**8**	**<1**
	Indet	0	1	0	0	**1**	**<1**
Femora	Complete	0	1	0	0	**1**	**<1**
	Proximal end	2	1	0	0	**3**	**<1**
	Midshaft	27	9	1	0	**37**	**2**
	Distal end	1	1	2	0	**4**	**<1**
Tibiae	Complete	1	2	0	0	**3**	**<1**
	Proximal end	1	1	0	0	**2**	**<1**
	Midshaft	25	23	0	0	**48**	**3**
	Distal end	7	5	1		**13**	**<1**
Fibula	Complete	0	0	0	0	**0**	**0**

	Proximal end	0		0	0	**0**	**0**
	Midshaft	1	0	0	0	**1**	**<1**
	Distal end	0	0	0	0	**0**	**0**
Metatarsi	Complete	2	0	0	0	**2**	**<1**
	Proximal end	6	5	0	0	**11**	**<1**
	Midshaft	29	6	0	0	**35**	**2**
	Distal end	1	0	0	0	**1**	**<1**
Metapodia	Complete	0	0	0	0	**0**	**0**
	Proximal end	2	1	0	0	**3**	**<1**
	Midshaft	8	7	0	0	**15**	**<1**
	Distal end	5	3	0	1	**9**	**<1**
Carpals/Tarsals		5	8	1	0	**14**	**<1**
Astragalus		7	0	0	0	**7**	**<1**
Calcanea		1	0	0	0	**1**	**<1**

Navicular bones		1	1	0	0	**2**	**<1**
Phalanges		15	4	1	0	**20**	**1**
LBN /MSH		363	97	3	0	**463**	**25**
NID		4	0	0	403	**407**	**22**
Others			0	0	3	**3**	**<1**
Total		**958**	**449**	**43**	**408**	**1858**	**100**
Percentage		**52**	**24**	**2**	**22**		

HWKEE contains a total number of 772 limb elements (Table 8). Of these, the majority (n=460, 60%) are from small mammals. The medium mammals are represented with a total of 281 (36%) limbs element followed by large mammals (n=31, 4%). The count of limbs elements (ULB, ILB, and ILLB, *sensu* Domínguez-Rodrigo1997; Domínguez-Rodrigo *et al.*, 2009) yielded the following results (Table8). Overall, the ILB (tibiae, and radii and ulnae) occur in high numbers (n=291, 39%) followed by LLB (metapodia) elements (n=272, 35%) and ULB elements (humeri and femora) elements (n=208, 26%). A Chi-Square Test was conducted of independence was conducted to assess the relationship between ULB and ILB. There were significant differences between the ULB and ILB (X^2(2, N=5) = 7,77336, *p*= 0.17). The Chi-Square Test results (X^2 (2, N=5) =3,0858, *p*= 0.70) show that the difference between ILB and LLB elements is minimal. The count of limb elements per interval revealed a nearly similar frequency of small and medium-size mammals in the LAS and LEMUTA intervals. However, limb elements of large mammals are higher in the LAS (n=22, 71%) interval than in the LEMUTA interval (n=9, 29%). Moreover, limb bone element representation per mammal size revealed a similar pattern in both the LAS and LEMUTA intervals, whereas ILB occurs in high numbers followed by LLB and ULB respectively.

Table 8: NISP Count of Upper, Intermediate, and Lower Limbs Element per animal size (*sensu* Domínguez-Rodrigo1997, Domínguez-Rodrigo*et al.*,2009)

Limb Category	**LAS**			**LEMUTA**			**Total**	**Percentage**
	Small	**Medium**	**Large**	**Small**	**Medium**	**Large**		
Upper Limbs (humeri and femora)	62	36	3	67	34	6	**208**	**26**
Intermediate Limbs (tibiae, radius + ulnae)	83	52	11	84	60	2	**292**	**39**
Lower Limbs (metapodia)	82	56	8	82	43	1	**272**	**35**
Total	**227**	**144**	**22**	**233**	**137**	**9**	**722**	**100**

There are differences in the frequency of upper *vs.* lower limbs based on animal size class (*sensu* Brain 1974, 1981; Bunn 1982) across the LAS and LEMUTA intervals (Table 9). The frequency of upper limb elements of mammal size class 1 is higher in the LEMUTA (n=40, 61%) than in the LAS (n=26, 39%) interval. For size classes 2 and 3, both LEMUTA and LAS interval lower limbs outnumber the upper limbs. The upper limb elements of mammal size 4 to 6 are less common (n=13, 4%) in both the LAS and LEMUTA.

Table 9: Frequency of Upper *vs.* Lower Limbs Element per Animal Size Class (*sensu* Brain 1974, 1981; Bunn 1982)

Upper Limbs					**Lower Limbs**				
Animal Size	**LAS**	**LEMUTA**	**Total**	**Percentage**	**Animal Size**	**LAS**	**LEMUTA**	**Total**	**Percentage**
1	26	40	**66**	**19**	1	17	36	**52**	**13**
2	71	76	**147**	**42**	2	102	80	**182**	**45**
3	62	64	**126**	**36**	3	78	72	**150**	**37**
4	3	5	**8**	**2**	4	6	0	**6**	**1**
5	1	0	**1**	**<1**	5	8	2	**10**	**2**
6	2	2	**4**	**1**	6	0	0	**0**	**0**
Total	**165**	**187**	**352**	**100**	**Total**	**211**	**190**	**401**	**100**

Percentage	**47**	**53**			**Percentage**	**53**	**47**		

4.4 Butchery

A total of 115 cut marks and 88 percussion marks were recorded on the LAS and the LEMUTA intervals (Table 9; Plate 2 and 3). The overall frequency of cut marks on taxonomically identifiable specimens is higher in the LEMUTA (n=69, 61%) than in the LAS interval (n=45, 39%). Most of the cutmarks on the entire sample (n=47, 34% for LEMUTA interval, and n=13, 11% for LAS interval) were recorded on the bone fragments that could not be assigned to a specific taxon. Of the remaining cut marks, the majority (n=55, 48%) were inflicted on Bovidae. Equidae, Suidae, Proboscidea, Hippotamidae, and Giraffidae recorded traces of cut marks, but in lesser numbers. One cut mark was recorded on a carnivore scapula recovered from the LAS interval. The count of percussion marks per taxa on the LAS and LEMUTA intervals yielded the following results. Most of the percussion marks (n=48, 56%) are present on long bone fragments that could not be assigned to specific taxa and the majority of these (n=37, 42%) are from the LEMUTA interval. The remaining percussion marks were inflicted on Bovidae (n=39, 41%) and Giraffidae (n=1, 1%). The Bovidae from the LEMUTA interval yielded the highest number of percussion marks (n=21, 24%) compared to the LAS interval (n=18, 20%). The inflicted percussion marks on both LAS and LEMUTA intervals are characterised by patches of microstriations and battered areas. Overall, the percussion marks on the LEMUTA interval contain 15 percussions notches, 6 isolated patches of microstriations, and one battered area. Similarly, the percussions marks on the LAS interval contain 24 percussions notches and three patches of microstriations only.

Table 9: NISP Count of Cut (CM) and Percussion Mark (PM) in LAS and LEMUTA Interval per Taxa

Taxa	**Count of CM per Interval**		**Total**	**Percentage**	**Count of PM per Interval**		**Total**	**Percentage**
	LAS	**LEMUTA**			**LAS**	**LEMUTA**		
Proboscidea	1	0	**1**	**1**	0	0	**0**	**0**
Primate	0	0	**0**	**0**	0	0	**0**	**0**
Carnivora	1	0	**0**	**1**	0	0	**0**	**0**
Rhinocerotidae	0	0	**0**	**0**	0	0	**0**	**0**
Equidae	2	4	**6**	**5**	0	0	**0**	**0**
Suidae	0	2	**2**	**1**	0	0	**0**	**0**
Hippotamidae	1	0	**1**	**1**	0	0	**0**	**0**
Giraffidae	1	1	**2**	**1**	1	0	**1**	**1**
Bovidae	27	28	**55**	**48**	18	21	**39**	**44**
NID/Indet	13	34	**47**	**41**	11	37	**48**	**55**
Total	**45**	**70**	**115**	**100**	**30**	**58**	**88**	**100**

Percentage	**39**	**61**	**100**		**34**	**66**	**100**	

Plate 2: An Example of Cut marks on a Long Bone (Source: Pante *et al.*, 2018**)**

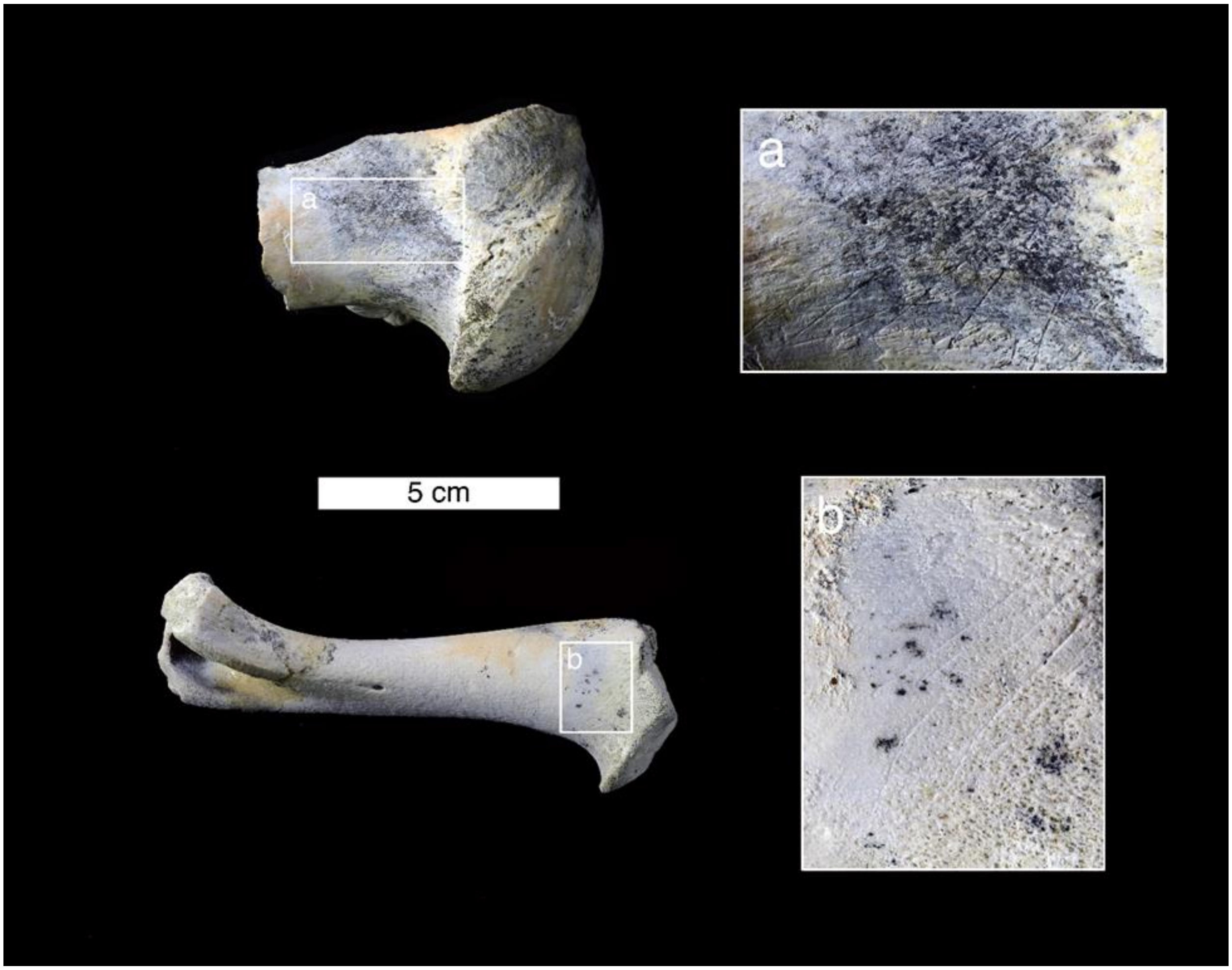
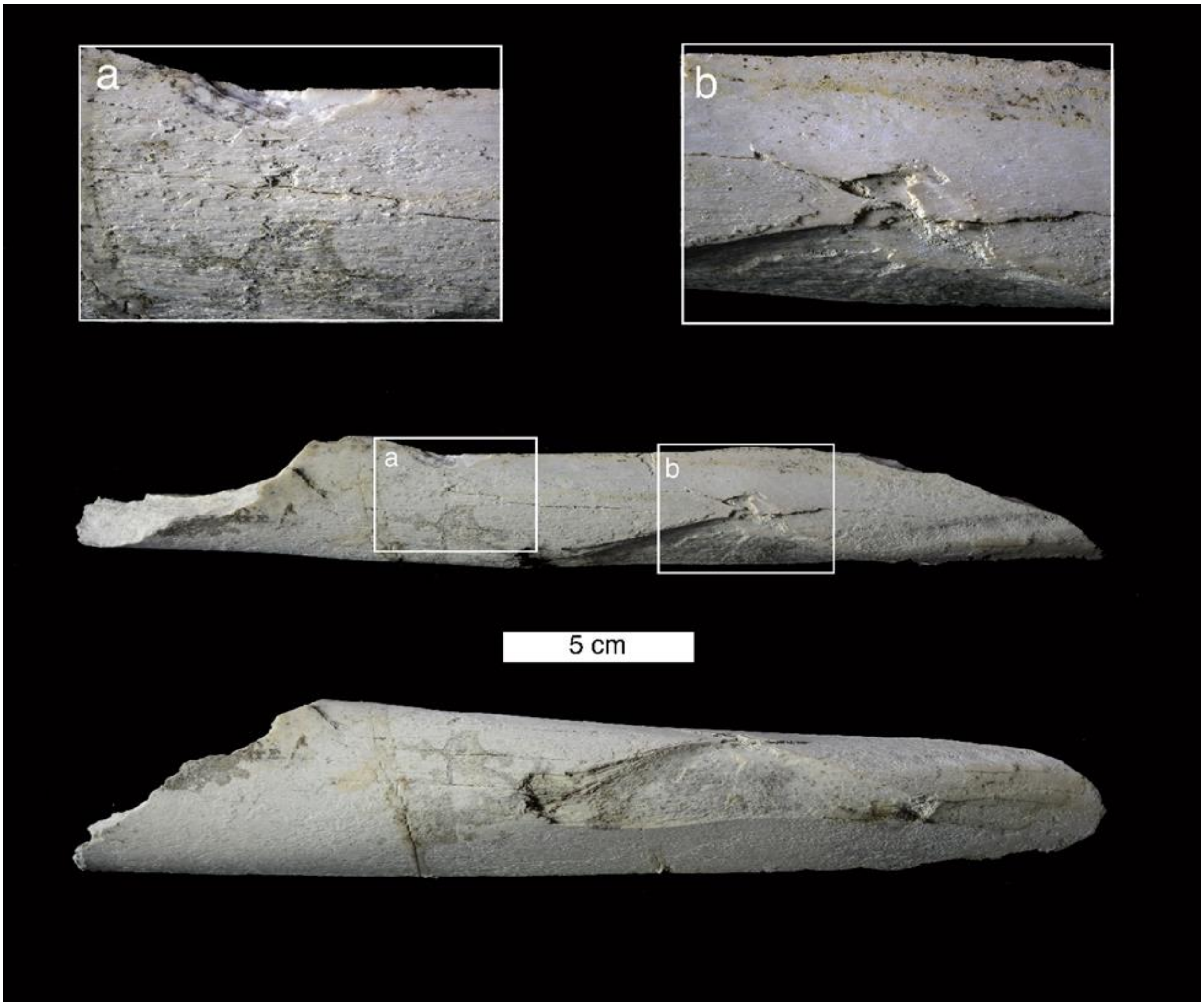


Plate 3: Example of Percussion Mark on a Midshaft Section (Source: Pante *et al.,* 2018)



There are some similarities and differences between the LAS and LEMUTA intervals based on the frequency of butchery marks per animal size (Table 10). Cut marks and percussions marks are higher on small mammals in LEMUTA (n=37, 32%) than in the LAS (n=17, 15%) intervals. Similarly, percussion marks on small mammal size are high on the LEMUTA (n=35,40%) than in the LAS (n=17,19%). Another notable difference is the higher frequency of cut marks on large mammals' bones in the LAS (n=8, 7%) *vs* LEMUTA (n=3, 3%) interval. Further, larger mammals' long bone LEMUTA intervals lack percussion marks.

Table 10: Frequency of Butchery Mark per Animal Size

Animal Size	**CM**		**Total**	**Percentage**	**PM**		**Total**	**Percentage**
	LAS	**LEMUTA**			**LAS**	**LEMUTA**		
Small (size 1, 2)	17	37	54	**47**	17	35	**52**	**59**
Medium (size 3)	21	29	50	**43**	11	23	**34**	**37**
Large	8	3	11	**10**	2	0	**2**	**2**
Total	**46**	**69**	**115**	**100**	**30**	**58**	**88**	
Percentage	**40**	**60**			**34**	**66**		**100**

The total number of 115 cut marks were recorded on the LAS and LEMUTA intervals (Table 11). Of these, most of the cut marks (17%) are on midshaft elements and tibiae (14%). Cutmarks are also nearly equally distributed on radii (10%), femora (9%), humeri, and ribs (7% each), metacarpi, and metatarsi (6% each), and mandibles (5%). The following elements, scapulae, radii and ulnae, ulnae (only), metapodia, phalanges, pelvises, lumbar and thoracic vertebrae, astragalus, and calcanea contain traces of cutmarks, but in lesser percentages. The remaining elements, including atlases, axis, sacrum, caudal and cervical vertebras as well as cranium, maxillae, fibulae, carpals/tarsals, and navicular bones do not contain traces of cut marks. The count of cut marks per skeletal element on the LAS *vs.* LEMUTA interval shows that skeletal elements on the LEMUTA interval contain most of the cut marks (LAS n=49, 40% *vs.* LEMUTA n=69, 60%). Traces of cut marks on phalanges (n=1, 1%) and metapodia (n=1, 1%) occur in the LEMUTA interval only. Similarly, cut marks on lumbar vertebrae (n=1,1%), pelvises (n=2, 1%), astragal (n=1,1%) and calcanea (n=1, 1%) were recorded in the LAS interval only. For the entire number of percussion marks (n=88) recorded on the sample (Table 11), the frequency of percussion marks is highest on the limb bone midshafts (31%) and femora (14%). The incidence of percussion marks is evenly distributed on metacarpi, tibiae, and metatarsi ranging between 10-11%. Percussion marks were also recorded on humeri (5%) metapodia (3%), ribs (2%), mandibles, and ulnae (1% each). No traces of percussion marks were recorded on the remaining skeletal elements. There are some differences in the frequency of percussion marks between LAS and LEMUTA intervals. In the LEMUTA interval, the incidence of percussion marks is higher on long bone midshafts, tibiae, femora, radii, and metatarsi than in the LAS interval. Notably, the incidence of percussion marks on rib (n=2, 2%), ulnae (n=1,1%) and humeri (n=4, 5%) was recorded on LEMUTA interval only. In contrast, the incidence of percussion marks on LAS interval is high for metatarsi (n=7, 8%) and metapodia (n=2, 2%). Further, percussion marks on the mandible (n=1,1%) were recorded on the LAS interval only.

Table 11: Frequency of Butchery Mark on LAS and LEMUTA Interval per Skeletal Element

Element	**CM**		**Total**	**Percentage**	**PM**		**Total**	**Percentage**
	LAS	LEMUT			LAS	LEMUT		

		A				A		
Horns	0	0	**0**	**0**	0	0	**0**	**0**
Cranium	0	0	**0**	**0**	0	0	**0**	**0**
Maxillae	0	0	**0**	**0**	0	0	**0**	**0**
Mandibles	4	2	**6**	**5**	1	0	**1**	**1**
Atlases	0	0	**0**	**0**	0	0	**0**	**0**
Axis	0	0	**0**	**0**	0	0	**0**	**0**
Cervical vertebrae	0	0	**0**	**0**	0	0	**0**	**0**
Thoracic vertebrae	1	1	**2**	**2**	0	0	**0**	**0**
Lumbar vertebrae	1	0	**1**	**1**	0	0	**0**	**0**
Caudal	0	0	**0**	**0**	0	0	**0**	**0**
Sacral vertebrae	0	0	**0**	**0**	0	0	**0**	**0**
Vertebrae indet	0	0	**0**	**0**	0	0	**0**	**0**

Pelvises	2	0	**2**	**2**	0	0	**0**	**0**
Scapulae	4	7	**10**	**3**	0	0	**0**	**0**
Ribs	3	5	**8**	**7**	0	2	**2**	**2**
Humeri	4	4	**8**	**7**	0	4	**4**	**5**
Radii and Ulnae	0	1	**1**	**1**	0	0	**0**	**0**
Radii	4	7	**11**	**10**	4	5	**9**	**10**
Ulnae	1	1	**2**	**2**	0	1	**1**	**1**
Metacarpi	1	6	**7**	**6**	3	6	**9**	**10**
Femora	4	6	**10**	**9**	2	10	**12**	**14**
Tibiae	6	10	**16**	**14**	3	7	**10**	**11**
Fibulae	0	0	**0**	**0**	0	0	**0**	**0**
Metatarsi	4	3	**7**	**6**	7	3	**10**	**11**
Metapodia	0	1	**1**	**1**	2	1	**3**	**3**
Carpals/Tarsals	0	0	**0**	**0**	0	0	**0**	**0**
Astragalus	1	0	**1**	**1**	0	0	**0**	**0**

Calcanea	1	0	**1**	**1**	0	0	**0**	**0**
Navicular bones	0	0	**0**	**0**	0	0	**0**	**0**
Phalanges	0	1	**1**	**1**	0	0	**0**	**0**
LBN /MSH	5	14	**19**	**17**	8	19	**27**	**31**
NID	0	0	**0**	**0**	0	0	**0**	**0**
Others	0	0	**0**	**0**	0	0	**0**	**0**
Total	**46**	**69**	**115**	**100**	**30**	**58**	**88**	**100**
Percentage	**40**	**61**			**34**	**66**		

The frequency of elements with cut marks per animal size (Table 12) is higher for medium-sized mammals (n=20, 44%) in the LAS interval, followed by small (n=17, 38%) and large mammals (n=8, 18%). Considering the specific location of cut marks on the skeletal elements, butchery marks on the mandible (n=4. 4%) are located on the horizontal ramii and mandibular symphyses. Cut marks on pelvises (n=2, 2%) were inflicted on the acetabulum. The traces of cut marks on the astragalus were inflicted on the trochlea. For the entire long bone elements (n=772), most of the midshaft section contains a high number of cut marks

Table 12: Table: Location of Cut Marked Element per Animal size in the LEMUTA Interval

Element	**Marked Location**	**Animal Size**		**Total per Marked Location**		**Grand Total**	**Percentage**
		Small	**Medium**	**Large**	**Total**		
Horns		0	0	0	**0**	**0**	**0**
Cranium		0	0	0	**0**	**0**	**0**
Maxillae		0	0	0	**0**	**0**	**0**
Mandibles		1	2	1	**4**	**4**	**3**
Atlases		0	0	0	**0**	**0**	**0**
Axis		0	0	0	**0**	**0**	**0**
Cervical vertebrae		0	0	0	**0**	**0**	**0**
Thoracic vertebrae		0	1	0	**1**	**1**	**1**
Lumbar vertebrae		0	1	0	**1**	**1**	**1**

Caudal vertebrae		0	0	0	**0**	**0**	**0**
Sacral vertebrae		0	0	0	**0**	**0**	**0**
Vertebrae indet		0	0	0	**0**	**0**	**0**
Pelvises		1	0	1	**2**	**2**	**2**
Scapulae		0	3	0	**3**	**3**	**3**
Ribs		1	2	0	**3**	**3**	**3**
Humeri	Complete	1	0	0	**1**	**4**	**3**
	Proximal end	1	1	1	**3**		
	Midshaft	0	0	0	**0**		
	Distal end	0	0	0	**0**		
Radii and Ulnae	Complete	0	0	0	**0**	**1**	**1**
	Proximal end	0	0	0	**0**		
	Midshaft	0	0	0	**0**		
	Distal end	0	0	0	**0**		

Radii	Complete		0	0	**0**	**7**	**9**
	Proximal end	0	0	0	**0**		
	Midshaft	2	1	1	**4**		
	Distal end	0	0	0	**0**		
Ulnae	Complete	0	0	0	**0**	**1**	**1**
	Proximal end	0	1	0	**1**		
	Midshaft	0	0	0	**0**		
	Distal end	0	0	0	**0**		
Metacarpi	Complete	0	0	0	**0**	**6**	**5**
	Proximal end	0	0	0	**0**		
	Midshaft	0	1	0	**1**		
	Distal end	0	0	0	**0**		
Femora	Complete	0	0	0	**0**	**6**	**5**
	Proximal end	0	0	0	**0**		

	Midshaft	0	3	0	**3**		
	Distal end	1	0	0	**1**		
Tibiae	Complete	0	0	0	**0**	**10**	**9**
	Proximal end	0	0	0	**0**		
	Midshaft	1	2	1	**4**		
	Distal end	0	1	1	**2**		
Fibula	Complete	0	0	0	**0**	**0**	
	Proximal end	0	0	0	**0**		
	Midshaft	0	0	0	**0**		
	Distal end	0	0	0	**0**		
Metatarsi	Complete	0	0	0	**0**	**3**	**3**
	Proximal end	0	0	0	**0**		
	Midshaft	3	0	0	**3**		
	Distal end	0	0	0	**0**		

Metapodia	Complete	0	0	0	**0**	**1**	**1**
	Proximal end	0	0	1	**1**		
	Midshaft		0	0	**0**		
	Distal end	0	0	0	**0**		
Carpals/Tarsals		0	0	0	**0**	**0**	**0**
Astragal	0	0	0	1	**1**	**1**	**1**
Calcanea	0	0	1	0	**1**	**1**	**1**
Navicular bones	0	0	0	0	**0**	**0**	**0**
Phalanges		0		0	**0**	**0**	**0**
LBN/Midshaft		5	0	0	**5**	**5**	**4**
NID		0	0	0	**0**	**0**	**0**
0thers		0	0	0	**0**	**0**	**0**
Total		**17**	**20**	**8**	**45**	**45**	**100**

There are some differences in the frequency of butchery marks per mammal size in the LEMUTA interval, compared to the LAS interval (Table 13). Cut marks are most dominant on small mammals (n=34, 49%), followed by medium (n=27, 39%) mammals. The frequency of cutmarks on the large mammals is low (n=3, 4%). Traces of cut marks recorded on mandible elements (n=2, 3%) occur on the horizontal ramus and mandibular symphysis. Cut marks on the scapulae (n=7,10%) were inflicted on the glenoid and blade. Considering the location of cut marks on the LEMUTA interval per long bone element and section, traces of cut marks are higher on the midshaft (n=42, 61%) followed by distal (n=6, 9%) and proximal ends (n=2, 3%). Moreover, 4 complete elements contain traces (6%) of cut marks. The location of cutmarks on skeletal elements per animal size in the LEMUTA interval revealed the following results. Most of the cut marks on the long bones element for small mammals were inflicted on midshafts (n=26,38%) followed by complete elements (n=3, 4%) and a distal end (n=1,1%). The incidence of cut marks on medium-sized mammals is also high on the midshaft elements (n=11,16%), followed by distal (n=5,7%) and the proximal ends (n=2, 3%), and one complete element. All cut marks for the large mammals were inflicted on midshaft elements.

Table 13: Location of Cut Marked Element per Animal size in the LEMUTA

Element	**Marked Location**	**Animal Size**			**Total per Marked Location**	**Grand Total**	**Percentage**
		Small	**Medium**	**Large**	**Total**		
Horns		0	0	0	**0**	**0**	**0**
Cranium		0	0	0	**0**	**0**	**0**

Maxillae		0	0	0	**0**	**0**	**0**
Mandibles		0	2	0	**2**	**2**	**3**
Atlases		0	0	0	**0**	**0**	**0**
Axis		0	0	0	**0**	**0**	**0**
Cervical vertebrae		0	0	0	**0**	**0**	**0**
Thoracic vertebrae		1		0	**1**	**1**	**1**
Lumbar vertebrae		0	0	0	**0**	**0**	**0**
Caudal vertebrae		0	0	0	**0**	**0**	**0**
Sacral vertebrae		0	0	0	**0**	**0**	**0**
Vertebrae indet		0	0	0	**0**	**0**	**0**
Pelvises		0	0	0	**0**	**0**	**0**
Scapulae		2	4	1	**7**	**7**	**10**
Ribs					**5**	**5**	**7**

Humeri	Complete	0	0	0	**0**	**4**	**6**
	Proximal end	0	0	0	**0**		
	Midshaft	2	1	0	**3**		
	Distal end	0	1	0	**1**		
Radii and Ulnae	Complete	0	0	0	**0**	**1**	**1**
	Proximal end	0	0	0	**0**		
	Midshaft	0	1	0	**1**		
	Distal end	0	0	0	**0**		
Radii	Complete	2	0	0	**2**	**7**	**10**
	Proximal end	0	2	0	**2**		
	Midshaft	2	0	1	**3**		
	Distal end	0	0	0	**0**		

Ulnae	Complete	0	0	0	**0**	**1**	**1**
	Proximal end	0	0	0	**0**		
	Midshaft	0	1	0	**1**		
	Distal end	0	0	0	**0**		
Metacarpi	Complete	0	0	0	**0**	**6**	**9**
	Proximal end	0	0	0	**0**		
	Midshaft	1	1	1	**3**		
	Distal end	1	2	0	**3**		
Femora	Complete	0	0	0	**0**	**6**	**9**
	Proximal end	0	0	0	**0**		
	Midshaft	4	2	0	**6**		
	Distal end	0	0	0	**0**		

Tibiae	Complete	0	0	0	**0**	**10**	**14**
	Proximal end	0	0	0	**0**		
	Midshaft	3	5	0	**8**		
	Distal end	0	2	0	**2**		
Fibula	Complete	0	0	0	**0**	**0**	**0**
	Proximal end	0	0	0	**0**		
	Midshaft	0	0	0	**0**		
	Distal end	0	0	0	**0**		
Metatarsi	Complete	1	0	0	**1**	**3**	
	Proximal end	0	0	0	**0**		
	Midshaft	2	0	0	**2**		
	Distal end	0	0	0	**0**		

Metapodia	Complete	0	0	0	**0**	**1**	**1**
	Proximal end	0	0	0	**0**		
	Midshaft	1	0	0	**1**		
	Distal end	0	0	0	**0**		
Carpals/Tarsals		0	0	0	**0**	**0**	**0**
Astragal		0	0	0	**0**	**0**	**0**
Calcanea		0	0	0	**0**	**0**	**0**
Navicular bones		0	0	0	**0**	**0**	**0**
Phalanges		0	1	0	**1**	**1**	**1**
LBN/Midshaft		12	2	0	**14**	**14**	**20**
NID		0	0	0	**0**	**0**	**0**
0thers		0	0	0	**0**	**0**	**0**
Total		**34**	**27**	**3**	**69**	**69**	**100**

The results of the frequency of cut marks located on limb elements per animal size is summarised in Table 14. Overall, the majority of cut marks were inflicted on ILB (n=27, 45%), ULB (n=18, 30%) and LILB (n=15, 25%). The frequency of cut marks is high on ULB and ILLB for small mammals compared to medium and large mammal sizes. Cut marks on ILB are higher on medium-sized mammals, followed by small and large mammals.

Table 14: Frequency of Cut Mark per Long Bone Limb Category

Limb Category	**LAS**			**LEMUTA**			**Total**	**Percentage**
	Small	Medium	Large	Small	Medium	Large		
ULB	3	4	1	6	4	0	**18**	**30**
ILB	3	4	3	7	9	1	**27**	**45**
LILB	6	3	1	3	1	1	**15**	**25**
Total	**12**	**11**	**5**	**16**	**14**	**2**	**60**	**100**

4.5 Tooth Marks

The HWKEE sample exhibits evidence of carnivore (n=456) and crocodile-induced tooth marks (n=11). Considering the frequency of carnivore and crocodile tooth marks per taxa, most of the induced marks occur on indeterminate (n=268, 58%) elements (Table 15). Of the remaining fauna, carnivore, and crocodile tooth marks on Bovidae outnumber (165, 36%) all the taxa. Equidae has the second-highest count of carnivore and crocodile tooth damage (n=16, 3%). Incidence of carnivore and crocodile tooth marks on the other taxa, namely Proboscidea, Primate, Carnivora, Rhinocrotidae, Suidae, Hippotamidae as well as Giraffidae are present, but in low numbers. There are notable differences betweencarnivore and crocodile inflicted-tooth marks per interval. Overall, the LEMUTA has more (n=255, 56%) carnivore tooth marks than in LAS interval (201,44%) and the pattern is reversed for crocodile tooth marks, n=7, 64% for LAS, and n=4, 36% for LEMUTA interval respectively.

Table 15: Count of Carnivore and Crocodile Tooth Marks in the LAS and LEMUTA interval per Taxa

Taxa	**Count of Carnivore TM per Interval**		**Total**	**Count of Crocodile TM per Interval**		**Total**
	LAS	LEMUTA		LAS	LEMUTA	
Proboscidea	2	0	**2**	0	0	**0**
primate	0	1	**1**	0	0	**0**
Carnivora	0	1	**1**	0	0	**0**
Rhinocerotidae	2	1	**3**	0	0	**0**
Equidae	3	10	**13**	3	0	**3**
Suidae	1	4	**5**	0	0	**0**
Hippotamidae	1	0	**1**	0	0	**0**
Giraffidae	3	2	**5**	0	0	**0**

Bovidae	75	87	**162**	1	2	**3**
NID/Indet	114	149	**263**	3	2	**5**
Total	**201**	**255**	**456**	**7**	**4**	**11**
Percentage	**44**	**56**	**100**	**64**	**36**	**100**

Carnivore tooth marking in the LAS and LEMUTA intervals (Table 16) is highest for small mammal sizes (261, 57%). This is followed by medium (n=164, 36%) and large-sized mammals (27, 6%). Conversely, crocodile tooth marks are highest on medium mammals (n=6, 55%) followed by small mammals (n=4, 36%). No crocodile tooth marks were recorded on the large mammals.

Table 16: Frequency of Carnivore and Crocodile TM per Animal Size

Animal Size	**Carnivore TM**		**Total**	**percentage**	**Crocodile TM**		**Total**	**Percentage**
	LAS	**LEMUTA**			**LAS**	**LEMUTA**		
Small (size1,2)	117	144	**261**	**57**	2	2	**4**	**36**
Medium (size 3)	66	98	**164**	**36**	5	1	**6**	**55**

Large	17	10	**27**	**6**	0		**0**	**0**
Indet	1	3	**4**	**1**	0	1	**1**	**9**
Total	**201**	**255**	**456**	**100**	**7**	**4**	**11**	**100**
Percentage	**44**	**56**						

Carnivore and crocodile tooth marks on LAS and LEMUTA intervals are present on the various skeletal elements (Table 17). The percentage of these marks is high on the midshaft limbs (22%) compared to the rest of the skeletal element (Table 17). The percentage of these marks is also evenly represented on ribs and humeri (9% each), radii, and tibiae (7% each).

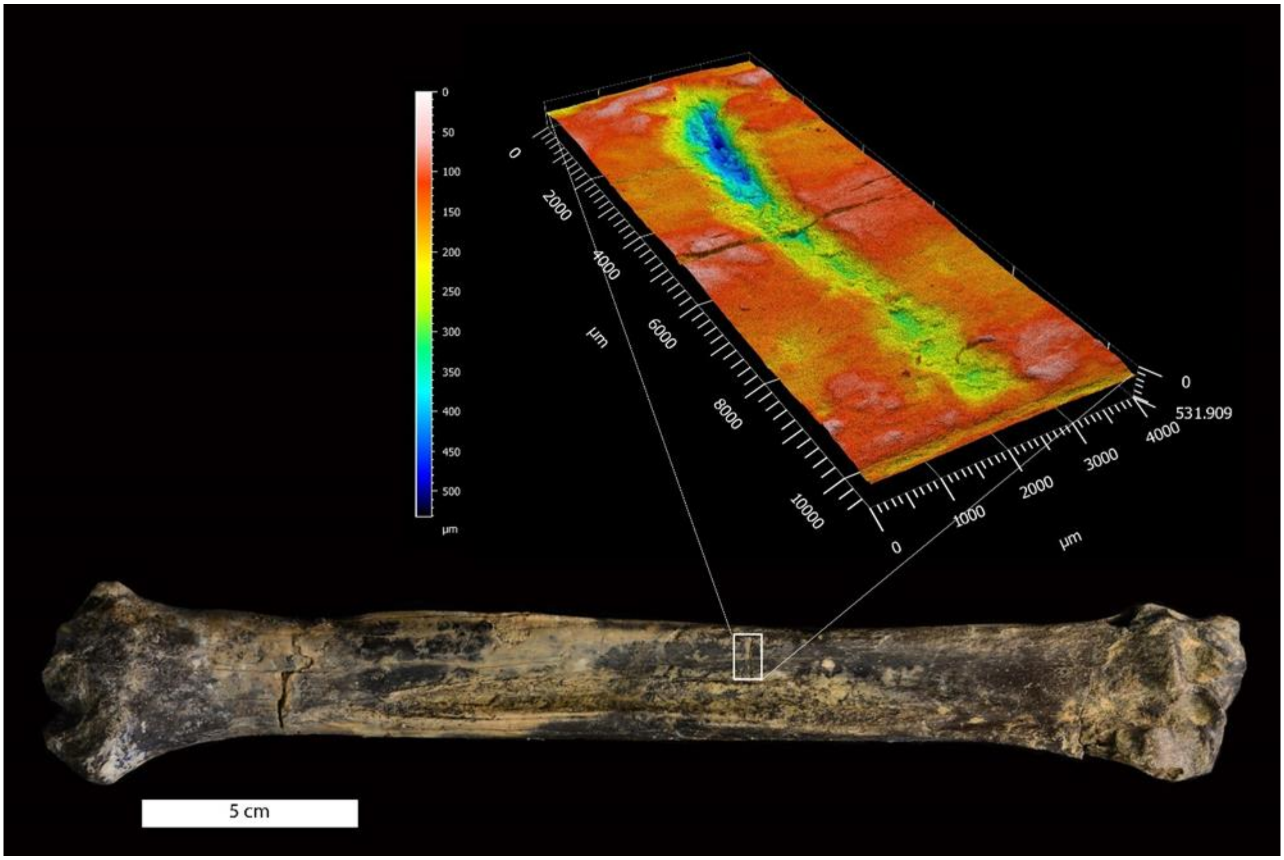
Table 17: Frequency of Tooth Mark in LAS and LEMUTA Interval per Skeletal Element

Element	**TM**		**Total**	**Percentage**
	LAS	**LEMUTA**		
Horns	5	2	7	**1**
Cranium	0	1	1	**<1**
Maxillae	3	1	4	**1**
Mandibles	5	6	11	**2**
Atlases	0	0	0	**0**

Axis	1	0	1	**<1**
Cervical vertebrae	5	4	9	**2**
Thoracic vertebrae	7	6	13	**3**
Lumbar vertebrae	7	1	8	**2**
Caudal	1	1	2	**<1**
Sacral vertebrae	1	2	3	**1**
Vertebrae indet	2	1	3	**1**
Pelvises	9	16	25	**5**
Scapulae	15	6	21	**4**
Ribs	18	23	41	**9**
Humeri	15	23	38	**9**
Radii and Ulnae	0	0	0	**0**
Radii	12	20	32	**7**
Ulnae	1	9	10	**2**
Metacarpi	7	14	21	**4**
Femora	12	15	27	**6**

Tibiae	18	17	35	**7**
Fibulae	0	0	0	**0**
Metatarsi	8	16	24	**5**
Metapodia	6	3	9	**2**
Carpals/Tarsals	1	2	3	**1**
Astragal	0	2	2	**<1**
Calcanea	2	0	2	**<1**
Navicular bones	0	0	0	**0**
Phalanges	3	3	6	**1**
LBN /MSH	43	60	103	**22**
NID	1	4	5	**1**
Others	0	1	1	**<1**
Total	**208**	**259**	**467**	**100**

Plate: An Example of a Carnivore Tooth Mark on a Long Bone (Source: Pante *et al.*, 2018)



Chapter Five

5 Data Interpretation and Discussion

5.1 Sample Composition

Large mammal bones at HWK EE are common in the LAS and LEMUTA intervals. Taphonomic analysis of the HWK EE fauna described the fauna at a broad family level (Pante *et al.,* 2018). The fauna includes various taxa such as Proboscidean, Primates, Carnivora, Bovidae, Equidae, Suidae, and Giraffidae. Overall, the majority of large mammals consumed by HWK EE hominins were bovids (Pante *et al.,* 2018; Pante and de la Torre 2018). Bovidae include various taxa, and these are common and well documented at other Olduvai ESA sites(e.g., Leakey 1971, Gentry and Gentry1978a, b; Bunn 1982;Bunn and Kroll 1986;Blumenschine *et al.,* 1991; Domínguez-Rodrigo *et al.,* 2009: Table 18). Bibi et *al.,* (2018) as well as Gentry and Gentry (1978a, b) provided additional Bovidae species recovered from HWK EE, based on dental and horncores remains. These include *Pelorovis oldowayensis Reck (*Extinct Giant Buffalo) *Connochaetes cf. C. gentry* (Wildebeest), *Tragelaphus strepsiceros* (Kudu)*, Alcelaphini 'small sp.,Parmularius maasaicus*(Topi/Hartebeest),*Hippotragus gigas* (Sable antelope), *Damaliscus niro* (Tsessebe), *Antidorcas recki* (Extinct Springbok) and *Gazella' sp. 'aff. rufifrons* (Red-fronted Gazelle). Rivals *et al*., (2018) add that alcelaphini and antilopini dental remains are the most dominant taxa in the HWK EE fauna sample. This pattern is also evident at other Olduvai ESA sites such as FLK Zinj, FLK NN, and BK (Leakey 1971; Gentry and Gentry1978a, b; Bunn 1982; Domínguez-Rodrigo *et al.,* 2009). Alcelaphini and antilopini consist of small and medium-sized ungulates, including wildebeest, waterbuck, and impala. This pattern accords with the result for long bones elements published by Pante *et al.* (2018) as well as data reported in this study. Representation of these taxa has strong implications to understand the paleoecology and potential meat resources for HWK EE hominins.

Table 18: Examples of Bovidae Taxa Recorded at Some Olduvai ESA Sites (Data from Leakey 1971, Gentry and Gentry1978a, b Bunn 1982, Domínguez-Rodrigo *et al.*, 2009).

Site 1= FLK Zinji, Site2 =FLK N6, Site 3 =FLKN1/2,Site 4=FLK NN2, Site 5 =BK

Taxa	**Common Name**	**Size Class**	**MNI**				
			Site 1	**Site 2**	**Site 3**	**Site 4**	**Site 5**
Antilopini	Tomson Gazelle etc.	1	6	4	10		
Antilopini	Impala etc.	2	1	3			
Alcelaphini	Wildebeest (small size)	3A	6	4	11	1	
Alcelaphini	Wildebeest, Hartebeest	3B	3	3	1	1	
Tragelaphini	Greater Kudu	3B	1	5	1		
Hippotragini	Oryx, Sable antelope	3B	1	1	2		
Bovine	Pelorovis	4-5	1	1	1		24

Bone Fragmentation

The fauna sample from HWK EE is fragmented and only a few specimens are complete. This result is expected because faunal remains from archaeological sites are often incomplete or fragmented (Blumenschine and Madrigal 1993; Reynard *et al.,* 2014; Reynard and Henshilwood 2018; Badenhorst *et al.,* 2019). The possible explanation for the high rate of fragmentary long bones at HWK EE is the involvement of crocodiles, carnivores, and hominins consuming various nutrients available in the long bone elements (de la Torre *et al.,* 2018a; Pante *et al.,* 2018). The HWK EE fauna sample displays evidence of butchery, terrestrial carnivore marks, crocodile-induced marks, as well as green fractures, suggesting they were broken by hominins or carnivores while fresh (Pante *et al.,* 2018). Several lines of evidence support the involvement of hominins, carnivores, and crocodiles in bone fragmentation at the site. In most Olduvai samples, hominins were breaking long bones to access bone marrow evidenced by the presence of hominin percussion marks (Blumenschine and Selvaggio 1988; Bunn 1981, 1982; Blumenschine 1995). HWK EE fauna sample recorded significant traces of hominin butchery marks. Therefore, butchering activities may have contributed to the bone fragmentation at the site.

Carnivore and crocodile tooth marks are also well preserved on the HWK EE sample. Crocodiles have a strong biting force that can tear carcasses apart and break bones into smaller pieces (Njau and Blumenschine 2006). Crocodiles often dismember and swallow parts of a carcass as a whole (Njau and Blumenschine 2006). However, they do not swallow un-ingested bones. When two or more crocodile shares a carcass, they crush it and produce fragments that are often deposited at the bottom of the river, lake, or water source (Njau and Blumenschine 2006). HWK EE was located near the lake margin (de la Torre *et al.,* 2018a). For this reason, it is possible that some of the fragments found on the HWK EE sample were produced during the crocodile feeding processes. Besides crocodiles, scavenging carnivores such as hyenas are known to break and destroy skeletal elements. The high number of midshaft on the fauna sample could be the influence of scavenging carnivores such as hyenas (Hutson and Cain 2008).

The bone assemblage from HWK EE indicates that hominins were acquiring and transporting different skeletal elements to the site (Pante *et al.,* 2018, Pante and de la Torre 2018; de la Torre *et al.,* 2018a). This is because the fauna sample is represented by all skeletal elements. However, there is a significant difference between the skeletal elements and portions of the mammal size classes. For instance, HWK EE long bones exhibit discrepancies in the representation of skeletal elements and portions in different mammal size classes. This discrepancy is common in the archaeological record because not all elements remain to survive or survive equally in the archaeological record (Klein 1989) because they have thick cortical walls and medullary cavities (Faith and Gordon 2006). For instance, long-bone ends have a low survival rate in the archaeological records because they have thin cortical walls and low-density, grease-rich cancellous portions which are often consumed by carnivores (Faith and Gordon 2006, Pante *et al.,* 2018). The HWK EE fauna sample recorded a high number of midshaft elements. Scavenging hyenas are known to produce a high rate of midshaft cylinders and fragments (Hutson and Cain 2008). The role of these carnivores may have contributed to the high number of midshaft portions recovered from the site (Pante and de la Torre 2018; Pante *et al.*, 2018). The rate of bone preservation is also subject to other taphonomic factors such as weathering and soil chemical composition (Brain 1981, Behrensmeyer 1978 and reference therein). Moreover, selective transport of carcass parts back to a home base, especially for larger taxa, may have influenced the skeletal representation at the site (Faith 2007; Faith *et al*., 2009).

Bone Accumulation by Hominins

One of the questions in this study explored is whether or not the locations and frequencies of cut marks on HWK EE fossils are consistent with hominins having primary or secondary access to carcasses. The HWK EE fauna sample has many butchery marks distributed across the various skeletal element of different taxa and mammal sizes. These marks are directly indicative of hominins feeding on carcasses of different sizes (Bunn 1982; Blumenschine 1988, 1995; Pante *et al.,* 2018). These traces carry important information on what type of resources hominins may have been exploited from various carcasses (Bunn 1981, 1982; Domínguez-Rodrigo1997; Blumenschine 1995). Overall, traces of cutmarks on the HWK EE fauna sample indicates that hominins were having primary access to small mammals as evidenced by the high frequency of the butchery marks. Evidence of butchery marks on the medium-sized mammals suggests that hominins had both primary and secondary access to carcasses. In both small and medium-sized mammals, cut marks are higher on the ULB and ILB. Further, the high frequency of cutmarks on the midshaft of small and medium-sized mammals indicates bulk or scrap flesh removal (Bunn 1982; Blumenschine 1987, 1995; Merritt 2011). The current study supports the accepted argument of various scholars (e.g., Bunn 1982, 1986; Domínguez-Rodrigo 1997Domínguez-Rodrigo*et al.,* 2009; Pante *et al.,* 2018) who have concluded that a high incidence of cut marks on the midshaft sections of small and medium-sized mammals indicate that hominins were having early access to carcasses with a substantial meat resource.

Apart from midshaft sections, HWK EE hominins left traces of butchery marks on other skeletal elements and portions including crania, mandibles, phalanges, ribs, and long bone-end. Cutmarks inflicted on different locations of bone elements are crucial in understanding different activities performed by hominins on carcasses (Bunn 1981, 1982; Merritt 2011; Leenen 2011). Evidence of butchery marks on the crania and mandibles suggest that hominins were processing head contents such as tongues (Blumenschine 1986; Leenen 2011). The feeding sequence model by non-hominin carnivores has shown that the head contents of a carcass are often consumed at the last stage of feeding (Blumenschine 1986, 1987). Thus, butchery marks on the crania and mandibles suggest secondary access to the carcass by hominins (Blumenschine 1987). Blumenschine (1987) argues that ESA hominins could have scavenged medium-sized carcasses left by large felids in riparian woodlands during the dry season with little or fewer flesh resources. However, bone marrow and crania resources were also available for scavenging hominins. Thus, it is likely that the presence of cutmarks on crania and mandibles of small and medium-sized mammal on the HWK EE sample represent secondary access to carcasses by hominins.

Traces of hominin butchery on ribs of small and medium mammals on the HWK EE fauna sample suggest that hominins at the site had primary access to the carcasses. This is supported by the ethological data on the feeding sequence carried out in the Serengeti National Park by Blumenschine (1986, 1987), as well as the fossil sample from the BK site in Olduvai Gorge reported by Pickering *et al.,* (2013). According to Blumenschine (1986), non-hominin carnivores consume prey ribcage tissue soon after kills. Thus, rib cage tissue (ribcage meat and upper viscera) of an animal carcass only occasionally survive after being fed on by non-hominin carnivores. Eviscerating butchery marks inflicted on the ventral and dorsal surfaces of the ribs indicate that hominins had access to the thoraxes of the carcasses (Nilssen, 2000; Pickering *et al.*, 2013). Moreover, the HWK EE fauna sample exhibits evidence of cut marks on proximal and distal articulations, indicating that hominins were disarticulating or dismembering carcass into manageable portions for transportation or consumption at the site (Bunn 1981, 1982).

Cutmarks on larger mammals beyond size three size 3 and 4were also exploited by hominins at HWK EE. However, traces of butchery marks on these mammals are few. This discrepancy could be attributed to several factors. First, only a small sample of larger mammals size was recovered from the site (also see: Pante and de la Torre 2018; Pante *et al.,* 2018). Second, butchery sometime leaves few marks on bones, even on larger animals (Parsons and Badenhorst 2004). Several factors cause variation in the frequency of butchery marks, including the experience of the butcher, butchering style, animal size, and type of the tools (Domínguez-Rodrigo 1997; Leenen 2011; Pobiner *et al.,* 2018; Badenhorst and Kimambo 2021).

Besides flesh, bone marrow is another appreciable source of nutrients that can be exploited from a carcass (Blumenschine 1988; Lupo and O'Connell 2002). HWK EE hominins were exploiting these resources from different taxa and mammal size classes. This is evidenced by the traces of percussion marks inflicted on different taxa and mammal sizes bones. There are some similarities and differences between the traces of cut marks and percussion marks based on taxa and mammal size class representation on the HWK EE fauna sample. First, the majority of percussion marks were recorded on bovids. These marks are dominant in small and medium-sized mammals. In contrast to an earlier analysis (Pante *et al.,* 2018), the results from the current study have shown that hominins at the site left evidence of percussion marks on long bones, mandibles, and ribs. Evidence of percussion on fossilised mandibles and ribs is rare in the archaeological record (Capaldo 1995). The most parsimonious explanation for traces of percussion marks on the mandibles could be related to access to bone marrow or opening the carcass skull to access crania contents, including the brain (Blumenschine 1987). Ribs have little marrow contents (Blumenschine 1987; Blumenschine and Selvaggio 1988). Thus, it is likely that percussion marks on the rib elements were created when hominins were trying to bash open rib cages to access viscera or internal organs.

Marrow exploitation is one of the main factors that determine which skeletal parts were mostly exploited or transported to the site (Jones and Metcalfe 1988; Bartram 1993). Carcass body part transport decisions are connected to nutritional values (Bunn 1986; O'Connell1988, Faith 2007; Faith *et al.*, 2009). Long-distance transport of a carcass often involves a selection of the body parts that have a high caloric return (Bunn 1986: 680). As Bunn (1986) pointed out, the fauna samples from Plio-Pleistocene sites in Eastern Africa are dominated by meaty appendicular elements compared to non-meaty elements such as vertebrae, ribs, crania, and pelvises (Bunn 1986). This implies that hominins were transporting appendicular skeletal parts for meat or marrow exploitation. Early access to a carcass would have provided hominins with access to fleshed appendicular elements with marrow content. On the other hand, if hominins gained secondary access to a carcass, they would have gained marrow or head contents (Blumenschine 1987). This, in turn, determines the rate of skeletal abundance at the site. HWK EE contains a high number of long bones/midshaft compared to the rest of the skeletal elements (Pante *et al.*, 2018, Pante and de la Torre 2018) As it has been pointed out earlier, the long bone elements contain traces of percussion marks. This suggests that hominins were likely exploiting or transporting long bone elements to the site. It should, however, be noted that other skeletal elements including crania, ribs, phalanges, and compact bones are also represented in the HWK EE fauna sample (also see Pante *et al.*, 2018). This may also suggest that carcasses were obtained close to the site or transported from a short distance (Bunn 1986; Faith 2007; Faith *et al.*, 2009).

Blumenschine (1986, 1987) proposed that abandoned lion kills offered potential and frequent scavenging opportunities encountered by hominins in the riparian woodlands. According to Blumenschine *et al.,* (1991:52), an abandoned lion kill offers, among other things, bone marrow and cranial resources (marrow and brain) to a scavenging hominin. Although this argument was supported by ethological and actualistic studies (Blumenschine 1986,1987, 1988) as well as ethnographic studies (Lupo and O'Connell 2002), the analysis of the timing for hominins' access to carcasses isoften restricted to long bone elements (e.g., Blumenschine 1995; Dominguez 1997; Pante *et al.,* 2018). One possible reason for this is the absence of butchery marks on other skeletal elements such as the ribs, pelvises, mandibles, and crania in most of the Olduvai Gorge ESA sites. The HWK EE fauna yielded evidence of percussion marks on the mandible elements. This is an indication that hominins at the site were exploiting marrow resources from skeletal elements other than long bones (Blumenschine1995).

One of the interesting findings is the absence of percussion marks on the Equidae and Suid specimens from the HWK EE fauna sample. This may suggest something about the cognitive ability of hominins on mammal long bone anatomy. Long bone marrow volumes differ across various taxa and mammal sizes (Blumenschine and Madrigal 1993). Binford (1978) as well as Blumenschine and Madrigal (1993) pointed out that the structure of the long bone cavity determines the volume of long bone marrow (also see Jones and Metcalfe 1988; Marshall and Pilgram 1991). Accordingly, Blumenschine and Madrigal (1993: 562) assert that there is an absolute lower marrow yield in suids and equids long bones. The reason for this is that some taxa (e. g., equid) contain densely cancellous bone throughout most of their midshaft sections (Blumenschine and Madrigal 1993: 560). For this reason, it may be the case that hominins at the HWK EE only selected specific species for long bone marrow extraction.

The Role of Carnivores

The palaeoecological data from mammal remains including bovids, equids, crocodiles, and fish indicate that HWK EE was characterised by an open and seasonal grassland habitat located at the margins of an alkaline lake during the LAS and LEMUTA intervals (Rivals *et al.,* 2018; Uno *et al.,* 2018; Bibi et *al.,* 2018). The presence of a water source likely attracted various mammals (Pante *et al.,* 2018). Large felids such as *Dinofelis* and *Panthera pardus* were present in the area during the middle bed II times (Leakey 1971). These large felids probably hunted a variety of animals which were later scavenged by hominins in the surrounding area. There was also possible tree coverage (Pante *et al.,* 2018Rivals *et al.,* 2018; Uno *et al.,* 2018; Bibi *et al.,* 2018). This environment may have been a potential habitat for leopards to store their kills. As mentioned by Cavallo and Blumenschine (1989) as well as Blumenschine and Cavallo (1992), leopards kill and store their prey in a tree to avoid competition from other carnivores or scavengers. Leopards often leave or abandon fleshed carcasses on a tree (Cavallo and Blumenschine 1989). This leaves an opportunity for an opportunistic scavenger to obtain carcasses with a substantial amount of flesh from small and medium-sized mammals (Blumenschine 1987; Cavallo and Blumenschine 1989; Blumenschine and Cavallo 1992; Blumenschine *et al.,* 1994). Hominins at HWK EE may have employed a similar strategy. The HWK EE fauna sample recorded the incidence of carnivore marks on a primate bone. Bibi *et al.,* (2018) report that among primate teeth remains recovered from HWK EE includes *Theropithecus oswaldi* (extinct baboons). Leopards are known to feed on primates, particularly baboons (Brain 1981; Thackeray 1990). It is possible that a leopard collected the primate bone in the HWK EE faunal sample. The contribution of leopards to the HWK EE fauna sample may be supported further by the fact that leopard kills consist of small ungulates and diverse smaller mammals that are available year-round (Blumenschine and Cavallo 1992: 93; Kruuk and Turner 1967).

Modern data of leopard prey from the Serengeti National Park shows that 76% of their prey consists of small mammals (Kruuk and Turner 1967: Table 19) and they rarely hunt big game, except for juveniles. According to Kruuk and Turner (1967), the Thomson gazelle is the most important prey for leopards, followed by impala and reedbuck. Smaller mammals such as jackals, rock hyraxes, spring hares, and birds are also frequently hunted by leopards (Thackeray 1990, Badenhorst *et al*. 2021). Since the HWK EE fauna sample is dominated by small and medium-sized mammals, it is possible that hominins at the site obtained meat from leopard kills. Access to fleshed carcasses from leopard kills may have contributed to the high frequency of cutmarks on the midshaft portion recorded on small and medium-sized mammals recovered from HWK EE.

Table 19: Examples of Modern Leopard Prey in Serengeti National Park (data modified from Kruuk and Turner 1967: 11)

Common Name	**Scientific Name**	**Mammals Size Class**	**Age Profile**	**Weight (kg)**	**Percentage**
Thompson Gazelle	*Eudorcas thomsonii*	1		16	27
Impala	*Aepyceros melampus*	2		40-75	16
Reedbuck	*Reduca redunca*	2		19-38	11
Blue Wildebeest	*Connochaetes taurinus*	3	Calf	20-100	4
			Yearling	100-350	4
Grand Gazelle	*Nanger granti*	2		45-65	4
Baboon	*Cercopithecidae*	1		20-28	4
Blue Wildebeest	*Connochaetes taurinus*	3	Adult	203 and above	2

Bushbuck	*Tragelaphus slyvactus*	2		45-80	2
Black-backed jackal	*Canis mesomelas*	<1		<10	2
Rock hyrax	*Procavia capensis*	<1		<10	2
Spring hare	*Pedetes capensis*	<1		<10	2
Python	*Pyhonidae*			<10	2

Equally possible, the HWK EE hominins may have scavenged larger carcasses from lion kills. In the modern Serengeti ecosystem, lions feed heavily on blue wildebeest (49%) and zebras (15%) (Kruuk and Turner 1967: 7). Kruuk and Turner (1967:8) add that gazelles contribute 10% to their diet, while other species contribute less than 2% each (Table20). Lions infrequently hunt big game (mammal size class 4-6, except for buffalos) (Kruuk and Turner 1967: 7). Based on this, it is likely that some of the medium mammals at HWK EE were hunted by lions, and subsequently scavenged by hominins for marrow. Gidna *et al.*, (2013: 170-171) showed that large felids consume nearly all flesh on some taxa. For instance, lions leave very little or no flesh/scraps resources on Equidae carcasses (Gidna *et al.*, 2013: 170-171). However, in a few instances, lions leave quite a bit of flesh on Equidae (zebra) carcasses (Pobiner 2015). Equids long bones have low marrow contents (Blumenschine and Madrigal 1993).Thus, hominins at the site were probably less interested in the de-fleshed carcass of some taxa (e.g., equids) because they had no resources to offer. Likely, infrequent hunting of big games (mammal size classes 4-6) by lions may have limited hominins scavenging opportunities on these resources at the site, resulting in their low representation in the sample. Further, isotopic and microwear analyses of mammal teeth from the site show that mammal remains during the LAS interval were accumulated and deposited during the dry season, a time when fresh grasses were absent (Uno *et al.,* 2018; Rivals *et al.,* 2018). For this reason, it is also possible that the lack of fresh grasses in the area may have resulted in nutritionally stressed grazing mammals, which may have been easily captured and exploited by hominins (Rivals *et al.*, 2018; Pante *et al.*, 2018).

Table 20: Example of Modern Common Prey for Lion in East Africa (Kruuk and Turner 1967; Scheel 1993)

Common Name	**Scientific Name**	**Mammals Size Class**	**Adult Female Body Weight (kg)**	**Percentage**
Wildebeest	*Connochaetes taurinus*	3	203	49%
Zebra	Equus quagga	3	219	15%
Grand gazelle	*Nanger Granti*	2	45-65	5%
Thompson Gazelle	*Eudorcas thomsonii*	1	16	5%
Buffalo	*Syncerus caffer*	4	446	5%
Warthog	*Phacochoerus africanus*	2	52	-
Top?	*Damaliscus lunatus*	3	108	<3%
Hartebeest	*Alcelaphus buselaphus*	3	126	2%

The dominance of long bone shafts, few articular ends, high incidence of carnivore tooth marking, as well as a high rate of bone fragmentation suggest hyena activities (Cruz-Uribe 1991; Pickering 2002). Like hominins, hyenas break long bones to access bone marrow. They are also known for damaging long bone ends (Cruz-Uribe 1991; Pickering 2002). This is supported by the fact that lions are flesh eaters and do not break the bones of larger mammals to access marrow (Gidna 2013). Other carnivores such as wild dogs and jackals also hunt or scavenge from large felid kills (Estes and Goddard 1967). Jackals and wild dogs may have left their tooth marks on the HWK EE fauna sample. However, a quantitative study of tooth marks dimension is needed to discriminate which specific carnivores inflicted tooth marks on the HWK EE samples.

Hominin and Carnivore Interaction at HWK EE

The interpretation of the incidence and location of butchery and the carnivore marks on the HWK EE fauna sample support a complex feeding sequence (Pante *et al.,* 2018). When the location and incidence of butchery marks are considered, the data support the Carnivore-Hominin-Carnivore model (Pante *et al.,* 2018). The high frequency of butchery marks on the assemblage of the small and medium-size mammals suggests that hominins preceded carnivores. The dominance of midshaft sections with high frequencies of carnivore modification marks on small and medium-sized mammals suggests that scavenging carnivores fed on carcasses abandoned by hominins. Crunching carnivores (hyenas) are known to gnaw long bone shafts and consume all epiphyses resulting in a high frequency of unconsumed complete limb bone shafts or cylinders (Binford *et al.,* 1988; Blumenschine 1988; Potts *et al.,* 1988; Cruz-Uribe 1991; Pickering 2002). Overall, HWK EE data contained a high number of midshaft portions with a high frequency of carnivore tooth marks. Thus, it is likely that hyenas may have consumed carcasses abandoned by hominins at the site.

Conclusion

Only a few experimental studies in Africa have been conducted to document traces and meaning of butchery marks on a complete skeleton and their implication for ESA hominin feeding behaviour (e.g., Brain 1967a, b; Capaldo 1995; Leenen 2011). Moreover, very few studies have attempted to examine primary or secondary access to carcasses using a variety of skeletal elements other than long bones from the fossil record (e.g., Capaldo 1995). The paucity of these studies is due to the lack of well-preserved and sampling biases on fossil remains from Eastern Africa ESA sites. Another reason is that the majority of ESA sites in Eastern Africa are a result of a mixture of bones from various accumulation events over long periods. The recent study has contributed to filling this gap by exploring traces of butchery marks on the HWK EE fauna sample. The HWK EE fauna sample is generally well preserved, and it contains traces of butchery and carnivore marks across various skeletal elements. These traces demonstrate that hominins at the site exploited a range of small to large mammal taxa and a variety of carcass resources including meaty appendicular elements, crania, and ribs. These resources were likely obtained from large felid kills of carnivores such as lions and leopards. Traces of butchery marks and percussion marks on the fauna sample support the hypothesis that hominins gained primary access to small mammals and secondary access to most of the medium and large mammals. The study has also shown that in absence of limb elements, butchery marks on well-preserved ribs and crania elements can be used to infer hominin access to carcasses. The HWK EE fauna sample has a high number of carnivore-inflicted tooth marks. Traces of butchery and carnivores marks the HWK EE fauna sample support two model i.e., Carnivore-Hominin-Carnivore and Carnivore-Hominins models of feeding sequence.

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