A GIS Image Analysis Approach to Documenting Oldowan Hominin Carcass Acquisition: Evidence from Kanjera South, FLK Zinj, and Neotaphonomic Models of Carnivore Bone Destruction

by

Jennifer Ann Parkinson

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ABSTRACT

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Adviser: Thomas Plummer

This dissertation presents taphonomic analyses of human- and carnivore-modified bone assemblages in order to elucidate the timing of hominin access to carcass resources in the African Early Pleistocene. One of the defining adaptations of the genus *Homo* is the routine incorporation of animal tissue into the diet with the aid of tools. As a nutritionally dense food source, the addition of meat to the diet is often associated with important changes in the morphology and behavior of early hominins. Yet the ecological and behavioral implications of meat consumption for hominins are not well understood. This study tests competing hypotheses of hominin carcass acquisition and hominin-carnivore competition through a comparative study of carnivore- and hominin-induced modifications in the zooarchaeological assemblages from Kanjera South, Kenya (ca. 2 Ma) and FLK I Level 22 (FLK Zinj), Olduvai Gorge, Tanzania (ca. 1.84 Ma). Patterns of bone preservation and the distribution of bone surface modifications from these two sites are analyzed within a comparative framework of new and existing taphonomic models. The new taphonomic models presented here include the largest modern bone assemblages documenting large felid and canid bone damage to date. A GIS image analysis method is used to analyze patterns of bone damage in experimental and archaeological assemblages. The GIS method originally described by Marean et al. (2001) is expanded here to incorporate ArcGIS Spatial Analyst tools, and this method is applied for the first time to analyze patterns of hominin and carnivore damage. Results of these analyses suggest hominins at both Kanjera South and FLK Zinj had early access to carcasses. At both sites, small and medium bovid carcasses may have been obtained through hunting, while remains of larger carcasses may have been obtained through active scavenging. Despite the evidence for early carcass access at both sites, overall frequencies of both hominin and carnivore modifications are lower at Kanjera South compared to FLK Zinj, suggesting differing competitive regimes at the two sites and potentially signaling differing behavioral strategies.

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INTRODUCTION

Arguably one of the major adaptive changes in hominin dietary evolution is the shift to increased consumption of animal tissue (including muscle, viscera, brains, and marrow). Meat eating by hominins is evidenced at Plio-Pleistocene archaeological sites in East Africa by butchery marks on bones of large mammals (Bunn 1981; Potts and Shipman 1981; Bunn 1983a; Bunn and Kroll 1986; the Plio-Pleistocene boundary is considered here to be 2.58 Ma following Gibbard et al. 2010). The earliest clear evidence for butchery is contemporaneous with the advent of the Oldowan stone tool industry at approximately 2.6 Ma, indicating that butchery was a component of the Oldowan as soon as tools appear (Semaw et al. 2003; Plummer 2004). The earliest evidence of cut marked bone associated with stone tools comes from Gona, Ethiopia (ca. 2.6 Ma) (Semaw et al. 2003) and the nearby locality of Bouri, Ethiopia (2.5 Ma) (de Heinzelin et al. 1999). More controversial evidence for cut marked bone which is not associated with stone tools dates to much earlier at ca. 3.4 Ma from Dikika, Ethiopia (McPherron et al. 2010). However, Domínguez-Rodrigo et al. (2010) have argued that the unclear taphonomic history of the Dikika finds call the authenticity of the reported cut marks into question, and that the marks may be trampling marks.

It has been traditionally assumed that *Homo habilis* was the maker of the Oldowan stone tools. In fact, this species name is taken from the Latin meaning “handy man” (Leakey et al. 1964). However, the earliest fossil evidence attributed to *Homo* dates to 2.33 Ma (the A.L. 666 maxilla from Hadar, Ethiopia) - nearly 300,000 years after the earliest stone tools are found (Kimbel et al. 1996). Plummer (2004) has suggested this means that either the antiquity of *Homo* has been underestimated or that an australopith on the lineage to *Homo* was the maker of the earliest Oldowan tools. The temporal range of the Oldowan (ca. 2.6-1.6 Ma) overlaps with three hominin genera: *Australopithecus*, *Paranthropus*, and *Homo* (Plummer 2004). The 2.5 Ma cut marked bones from Bouri are stratigraphically associated with *Australopithecus gahri* (Asfaw et al. 1999; de Heinzelin et al. 1999), and this has led some to suggest *A. gahri* was the first tool maker (Semaw et al. 2003). *Paranthropus* also overlaps Oldowan archaeological occurrences in both East and South Africa, and is found in the same archaeological level at Olduvai Gorge (FLK I, Level 22) with butchered bone as well as remains of *Homo habilis* (Leakey 1971). While the number of species making early stone tools is unclear, it is generally agreed that *Homo habilis* and early African *Homo erectus* (=*ergaster*) made Oldowan tools (Plummer 2004; but see Susman 1991). *Homo erectus*, known from 1.8 Ma, is clearly associated with stone tools (Isaac 1997; Anton 2003). *Homo habilis* is recognized now by most to encompass two species: a large, megadont form (*Homo rudolfensis*) and a more gracile form (*Homo habilis* sensu stricto) (Chamberlain 1989; Wood 1992). Because the ancestor of *Homo erectus* almost certainly would have used stone tools, evidence for an ancestor-descendant relationship between *Homo habilis* sensu stricto and *Homo erectus* (Strait et. al 1997) strongly suggests *H. habilis* sensu stricto was a tool maker. *H. habilis* sensu stricto was probably responsible for forming archaeological assemblages beginning around 2.3 Ma, while both *H. habilis* sensu stricto and *H. erectus* formed sites during the period in which they temporally overlap beginning at 1.8 Ma when *H. erectus* appears (Plummer 2004; Plummer et al. 2009b). As taxonomic attribution for the makers of the Oldowan is difficult to assign and because it is likely that multiple species of tool-makers existed during the Plio-Pleistocene, I will refer to them here as Oldowan hominins, with the assumption that the ca. 2 Ma tool-makers at FLK Zinj and Kanjera South were early members of the genus *Homo*.

Some important morphological changes took place in the hominin lineage with the transition from an *Australopithecus*-grade hominin to *Homo erectus*. These include an increase in body size, an increase in brain size and a shift toward dedicated bipedalism. These changes suggest an increased energy requirement for early members of the genus *Homo* (Aiello and Wheeler 1995; Aiello and Wells 2002; Leonard and Robertson 1994; Leonard et al. 2003). Increased energy expenditure would have required a higher quality diet. As a nutritionally dense food source, animal tissue may have been a key resource supporting increased nutritional requirements (Milton 1999; Aiello and Wells 2002). It is assumed that like other primates, hominins also consumed plant foods including fruits, seeds, nuts and plant underground storage organs. An increased consumption of animal tissue would have been a supplement to these plant foods (Plummer 2004). Meat comprises approximately one third to one half of the mean annual caloric intake in modern African hunter gatherer groups (e.g., Lee and DeVore 1968; O'Connell et al. 2002). Meat probably comprised less of the diet of early *Homo*, but it was likely a key source of protein and fat, and may have been a critical resource during times of seasonal plant food shortages (Foley 1987).

Evolutionary changes in the hominin lineage in the Late Pliocene are thought to have been spurred by environmental changes between 2.0-3.0 Ma. The onset of glaciation in the northern hemisphere during this time resulted in a cooling and drying trend in Africa, which ultimately led to an increase in grasslands relative to forest habitats, and likely resulted in an increase in overall habitat heterogeneity (deMenocal 1995; Cerling 1992; Bobe et al. 2002; Wynn 2004; Bobe 2006; Potts 2012; Magill et al. 2013). The decrease in forest habitats at this time would have resulted in a decrease in the availability of fruits and nuts which were probably main components of the australopith diet (Sept 1986; Foley 1987). This likely increased competition among hominins over forest-derived plant foods. Competition may have been further exacerbated by an increase in rainfall seasonality, which in modern African settings is associated with plant food shortages during dry seasons (Foley 1987). The proportional increase in grassland habitats beginning in the Late Pliocene would have provided few plant food resources for hominins, but grasslands do support large populations of grazing ungulates (Wynn 2004), and archaeological evidence shows that hominins had begun to exploit these new food sources by the Early Pleistocene.

It is well established that Oldowan hominins were at times butchering large mammal carcasses. However, the method of carcass acquisition (i.e., hunting vs. scavenging), the timing of access to carcass resources, the degree of carcass completeness (fleshed vs. defleshed) at the time of hominin access, as well as the importance of meat in the diet of Oldowan hominins is less certain. Research on this topic has revolved around a central debate over hunting versus scavenging (Binford 1985; Potts 1988; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003). Opinions regarding this debate vary widely from envisioning hominins as marginal scavengers of flesh scraps and within-bone resources left on carcasses of carnivore kills (Binford 1981, 1986, 1988; Shipman 1986; Blumenschine 1987, 1995; Blumenschine and Cavallo 1992; Capaldo 1995, 1997; Selvaggio 1994b, 1998; Pante et al. 2012) to aggressive scavengers of large mammal carcasses and possibly hunters of small mammals (Bunn and Kroll 1986; Potts 1988; Bunn and Ezzo 1993; Oliver 1994; Domínguez-Rodrigo 2002, 2009; Plummer 2004; Domínguez-Rodrigo et al. 2007; Ferraro et al. 2013).

The hunting-versus-scavenging debate has important implications for understanding the evolution of the genus *Homo*, not only in terms of diet, but also in terms of behavior (Domínguez-Rodrigo et al. 2007). Animal tissue is not only a potentially nutritionally important resource, but also a socially important one. Evidence for early carcass access could imply regular meat eating and instances of food surplus, which may have promoted food sharing or other cooperative behaviors that are important in modern human groups (Isaac 1978; Kaplan and Hill 1985; Hawkes et al. 2001; Marlowe 2001). Evidence for late carcass access would imply a more passive scavenging strategy, suggesting hominins were low ranking within the group of animals consuming large mammalian prey (Blumenschine 1995), and the social implications above may not apply (O'Connell et al. 2002). Given this, reconstructions of the potential amount of meat in the hominin diet and its method of acquisition have implications for interpreting hominin dietary as well as social evolution.

When hominins first began to encroach on the carnivore guild, they would not have been top predators, but gradually would have had to evolve strategies to survive in their new competitive environment (Lewis and Werdelin 2007). Brantingham (1998) has argued that hominin competition with carnivores for shared limited resources (i.e., large mammalian carcasses) led to coevolution in the form of resource partitioning and competition-driven character displacement. He argued that the advent of stone tool technology acted as a form of character displacement eventually allowing hominins to enter a centrally-positioned niche within the predatory guild.

It has long been argued that the increase in meat eating and concurrent increase in brain size allowed for an increase in social complexity in early hominins. This idea was first explicitly articulated in Lee and DeVore's (1968) *Man the Hunter* volume which resulted from a conference held in Chicago in 1966. Papers in this volume presented ethnographic evidence to support a claim that hunting has been an integral part of the evolution of modern human behavior. The hunting paradigm held sway in the field of paleoanthropology for more than a decade before being seriously questioned by researchers focused on the use of experimental methods and work grounded in archaeological rather than ethnographic evidence (Binford 1981; Brain 1981). Isaac's (1971, 1978) influential "home base" hypothesis argued that cooperation related to food acquisition may have been more important in shaping modern human behavior than the aggressive behaviors related to hunting that the "man the hunter" hypothesis focused on. The "home base" hypothesis argued that hominins would have used a base camp or central place from which they dispersed and returned to on a daily basis. According Isaac, the use of a home base would have entailed a sexual division of labor in which males hunted or scavenged and females gathered plant foods. These foods would have then been brought back to the home base to be shared.

In a subsequent hypothesis of Oldowan site formation, Schick (1987) argued that large sites where dense accumulations of stone tools and bones are found represent repeatedly-visited rich foraging areas where hominins had easy access to stone raw material. If raw material was readily available nearby, transport costs could have been lessened by discarding lithics at the site where bone refuse and stone tools would have accumulated over time. Schick argued that smaller sites may represent just a few behavioral events, or may represent areas were stone raw material was less common, so artifacts were transported away rather than being discarded on site. Bunn (1991) has argued for a similar "favored place" scenario to explain Oldowan site formation, where he envisioned these sites as repeatedly visited safe areas where hominins could rest, socialize, consume transported carcass parts, and make tools. Other models have argued Oldowan zooarchaeological sites represent places where hominins were able to take refuge and defend their resources from carnivores or other groups of hominins (Rose and Marshall 1996; Blumenschine 1987, 1991), or caches of stone raw material where carcasses were brought for processing (Potts 1984, 1991). These subsequent models did not assume food sharing or sexual division of labor as in Isaac's home base model. However, Oliver (1994) has argued that repeated use of sites as a predator avoidance strategy by hominins with altricial young would have provided a selective context for the development of food transport, provisioning, and food-sharing behaviors in hominins. Presently, there is still little agreement among researchers on the nature and function of Oldowan hominin archaeological sites. As such, answering questions about the mode of hominin carcass acquisition at these sites has direct bearing on our ability to understand other aspects of hominin socioecology.

In this dissertation I examine the issue of hominin meat acquisition through an analysis of carnivore- and hominin-induced damage on the approximately 2 Ma archaeofaunal assemblage from Kanjera South, Kenya and the slightly younger assemblage from FLK I Level 22 (FLK Zinj), Olduvai Gorge, Tanzania. I analyze these assemblages using an experimental framework of new and existing taphonomic models replicating how carnivores and humans damage bone. The following provides a summary of the structure of this dissertation.

In Chapters 1 and 2, I report on new experimental research on bone modification patterns and tooth mark frequencies produced by large canids (multiple species of wolves) and large felids (lions and tigers). This work adds to the growing body of neotaphonomic literature on carnivore bone modification by providing the largest experimental assemblage of bones modified by these taxa to date. Neotaphonomic is defined here following Hill (1978) to include experimental observations of modern processes of bone decay and deposition designed to test interpretations of the fossil record. I use a GIS image analysis approach to characterize bone damage patterns (including bone surface damage and fragmentation) in the experimental assemblages in this study. This research presents the first application of GIS image analysis to study patterns of carnivore bone modification. I expand on the method originally described by Marean and colleagues (Nilssen 2000; Marean et al. 2001; Abe et al. 2002) by incorporating use of the ArcGIS Spatial Analyst tools to identify areas of significantly dense tooth marking across elements. In addition to the neotaphonomic assemblages of carnivore bone modification that I present here, I use GIS image analysis to characterize damage patterns observed in Blumenschine's (1995) previously studied experimental bone assemblages which model differing scenarios of carnivore-only, hominin-only and hominin-first access to carcasses.

In the second part of this dissertation, I use the framework of GIS experimental models I have created to interpret bone modification patterning in the Kanjera South (Chapter 3) and FLK Zinj (Chapter 4) archaeofaunal assemblages. The aim of this aspect of my research is to address questions about the order of access by hominins and carnivores to carcass resources at these sites in order evaluate Oldowan hominin foraging ecology and competitive interactions with carnivores. My results indicate that at Kanjera South, the pattern of bone preservation for small and medium bovids (size 1-3a, following Bunn 1982) is similar to GIS-generated models based on experimental bone assemblages that were first butchered and hammerstone fractured by humans, and subsequently scavenged by carnivores. The distribution of bone modifications on the Kanjera fauna revealed in the GIS analysis also suggests hominins had early access to small and medium bovids. Large bovids are not as well represented at Kanjera, and so bone damage patterns are difficult to characterize, but evidence presented here suggests hominins may have been scavenging the larger bovids. These results lend further support to the interpretation of early access of size 1 and 2 bovids that has been made for this site by Ferraro et al. (2013).

The interpretation of the nature of hominin involvement in the well-studied archaeofaunal assemblage from FLK Zinj has been a subject of some disagreement in the literature (Bunn 1986; Blumenschine 1995; Oliver 1994; Selvaggio 1994b, 1998; Capaldo 1997; Dominguez-Rodrigo and Barba 2006; Dominguez-Rodrigo et al. 2007; Blumenschine et al. 2007; Pante et al. 2012). The new GIS image analysis data I present here for the FLK Zinj assemblage suggest early access by hominins to fleshed carcasses at FLK Zinj, particularly of smaller prey, which may have been acquired through hunting. Damage patterns on larger carcasses are more difficult to interpret, but are not inconsistent with early access (hunting or aggressive scavenging). Further, a reanalysis of carnivore tooth mark frequencies in the FLK Zinj assemblage corroborate those cited by Domínguez-Rodrigo and colleagues (2007), lending additional support to an early access scenario for hominins.

CHAPTER 1. A GIS-Based Approach to Documenting Large Canid Damage to Bones

ABSTRACT

Experimental studies of modern carnivore tooth marking patterns are integral to understanding the nature of carnivore involvement in archaeological bone assemblages. However, modern bone damage data for most carnivore taxa are limited. This is particularly true for canids. Here I present bone damage data collected from feeding experiments conducted with Mexican Gray Wolves (*Canis lupus baileyi*) and Red Wolves (*Canis rufus*). This is the largest experimental assemblage reported for canids to date. I use the GIS image analysis approach described by Marean et al. (2001) to document bone preservation and tooth mark distribution, which is the first application of this approach to a carnivore-modified bone assemblage. Further, I introduce the use of the ArcGIS Spatial Analyst to identify significant concentrations of bone modifications. My results show the distribution of tooth pits varies considerably across elements as well as across different portions of the same element, and that significant clusters of tooth pits occur on all long bones. My results suggest that with a large enough sample, the GIS Spatial Analyst can be a useful tool for analyzing the distribution of bone modifications with greater resolution than previous methods. This method facilitates comparisons between experimental and fossil assemblages which may aid in identifying the timing of access to carcasses by carnivores involved in modifying fossil assemblages. Finally, the use of this rigorous methodology is a step toward increasing standardization in methods of taphonomic analysis.

INTRODUCTION

Bone damage patterns created on prey animals by modern carnivores can be used as a proxy to interpret the involvement of extinct carnivores in archaeological bone assemblages. This question has been particularly pertinent to researchers interested not only in carnivore behavior, but also in assessing potential competitive interactions between carnivores and hominins over the course of human evolution. Unfortunately, modern experimental datasets for carnivore-induced modifications are limited. This is particularly true for canids, which were potentially important agents of bone modification and assemblage formation during the Plio-Pleistocene of Eurasia, North America and Africa.

Taphonomic studies of carnivore bone modification have paid particular attention to patterns produced by hyaenids (Blumenschine 1988; Marean and Spencer 1991; Marean et al. 1992; Blumenschine and Marean 1993; Capaldo 1997; Faith 2007; Kuhn et al. 2009) and felids (Domínguez-Rodrigo 1999; Domínguez-Rodrigo and Barba 2006; Pobiner 2007; Gidna et al. 2013) in African settings. However, little attention has been paid to the bone modification signature of large canids. Canids were an important part of the Pleistocene large carnivoran paleoguild, and some were potentially high-level competitors (Brugal and Boudadi-Maligne 2011). Although large canid fossils overlap with modern and pre-modern human archaeological occurrences, the degree to which large canids may have competed with and influenced food acquisition behaviors of pre-modern humans is not well understood.

This study presents new bone damage data from feeding experiments conducted with large canids. I use a GIS image analysis method to record and analyze bone preservation patterns and surface modifications in this assemblage. This method, developed by Marean et al. (2001), provides a powerful means of analyzing and archiving large amounts of bone fragment data. Using the GIS image analysis method has several advantages. 1) It allows for more accurate recording and better visual representation of bone surface modifications, which can be examined relative to the degree of preservation of particular element portions. 2) The powerful relational database function of ArcGIS software provides a means of organizing and analyzing data on a finer scale than would otherwise be possible, including damage density and the spatial relationship of damage to anatomical markers. 3) This approach can provide a means of standardizing zooarchaeological data collection methods.

Pleistocene Large Canid Distribution

Canids are abundant and taxonomically diverse throughout the Plio-Pleistocene record of Europe (Brugal and Boudadi-Maligne 2011). Large canids appear in the Western European record just below the Plio-Pleistocene boundary at around 2 Ma (this is the original boundary designation prior to the recent revision by Gibbard et al. 2010), following the well known European faunal turnover ‘wolf-event’ (Azzaroli 1983; Torre et al. 1992). This turnover is marked by a major extinction of carnivores in Europe, including the cursorial hyaenid *Chasmaporthetes lunensis*, the appearance of the large hyaenid *Pachycrocuta brevirostris,* and a radiation of large canid species (Martínez-Navarro and Rook 2003; Sardella and Palombo 2007).

Some of the earliest canids in Europe that potentially overlap pre-modern humans are the wolf-like *Canis etruscus* and *Canis mosbachensis* (Fig. 1.1). Although their taxonomy is disputed, these species are potentially a single lineage that persisted from the Early through the Middle Pleistocene. The modern *Canis lupus* lineage appears in the Late Pleistocene (Brugal and Boudadi-Maligne 2011). Dental morphometric analyses show that the slicing component of the *C. lupus* dentition is more developed than the crushing component, suggesting that wolves have a more carnivorous diet than these earlier species of *Canis* (Brugal and Boudadi-Maligne 2011).

Two other genera of large, hyper-carnivorous (flesh specialist) canids are present in Pleistocene Eurasia: *Cuon* (the Asiatic wild dog) and *Xenocyon*, which some consider to be the same genus as the African hunting dog *Lycaon* (Martínez-Navarro and Rook 2003). The genus *Xenocyon* includes two chronospecies - *Xenocyon* (=*Lycaon*) *falconeri* and *Xenocyon* (=*Lycaon*) *lyconoides* - which persisted in Eurasia until the Middle Pleistocene (Martínez-Navarro and Rook 2003). These earlier species of lycaon-like canids were larger in size than extant African

Figure 1.1. Distribution of large canid species during the Late Pliocene and Pleistocene.

Arrows indicate chronospecies. Dotted line indicates insecure record. Age ranges for species based on the following: C. dirus (Dundas 1999); C. lupus, Cuon, C. etruscus, C. mosbachensis (Brugal & Boudadi-Maligne 2011); C. chihliensis (Tong et al. 2012); X. falconeri; X. lycanoides, L. pictus (Martínez-Navarro & Rook 2003); L. sekowei (Hartsone-Rose et al. 2010)

hunting dogs and more comparable to modern wolves, with hyper-carnivorous dental morphology (Martínez-Navarro and Rook 2003).

The African fossil record of canids is comparatively small. The earliest larger-sized canids (i.e., larger than jackal-sized) from Africa are known at Ain Hanech, Algeria (1.8 Ma) (Sahnouni et al. 2002), and also from Kromdraai Member A (ca. 1.5 Ma) (Turner 1986; Geraads 2011), Sterkfontein Valley Coopers D (1.6-1.9 Ma) and Gladysvale (1.0 Ma) (Hartstone-Rose et al. 2010), and Olduvai Beds I (ca. 1.84) and II (ca. 1.75-1.20) (Ewer 1965). These African species have been published under various names (*Canis atrox, Canis africanus*), but they likely represent the same species (Geraads 2011). Martínez-Navarro and Rook (2003) have synonymized *Canis africanus* with Eurasian *Xenocyon lycanoides* as a plausible ancestor for modern *Lycaon*. The modern African hunting dog (*Lycaon pictus*) is smaller in size than these fossil species and relatively recent in origin (Werdelin and Lewis 2005). Although larger in size, the earlier Pleistocene forms in Africa display a dental morphological pattern suggestive of less hyper-carnivory than modern *L. pictus* (Martínez-Navarro and Rook 2003).

The North American large canid fossil record is much better known than the African record. The dire wolf (*Canis dirus*) was one of the most common mammalian species during the Rancholabrean Land Mammal Age of North America (Middle to Late Pleistocene) and has been reported from 136 localities (Dundas 1999). The dire wolf was similar in size to *Canis lupus*, but more heavily built, and with a significantly more robust dentition (Kurtén and Anderson 1980). There has been some debate over the feeding behavior of this species. Some have suggested *C. dirus* was capable of crushing bone and may have filled a hyena-like scavenging niche in North America (Biknevicius and Ruff 1992). Others, however, have argued that although larger in size, the craniofacial and dental morphology closely mirror *C. lupus*, suggesting a wolf-like hunting and feeding behavior (Anyonge and Baker 2006). *Canis dirus* was among the taxa that succumbed to the megafaunal extinction at the end of the Pleistocene. Modern *Canis lupus*, which arose in the Old World, is not seen in North America until the Late Pleistocene, but is one of the most widely distributed land mammals after that time. Its historic distribution covered the majority of the Northern hemisphere, stretching from the Arctic through northern Mexico, as well as in Eurasia and North Africa (Kurtén and Anderson 1980; Feldhamer et al. 2003; Gaubert et al. 2012).

Canids as Potential Bone Modifying Agents, and Taphonomic Research to Date

The above overview shows that large canids were present during and overlapping periods of human occupation at points of critical interest in human evolutionary history, and thus were potentially important contributors to or modifiers of the Pleistocene zooarchaeological record. In part, the paucity of taphonomic research on large canids is due to their underrepresentation at African sites relative to other large carnivore species. Much of the research on carnivore bone modification has been conducted in African contexts with the aim of answering questions regarding the origins of hominin meat-eating behaviors, and so has focused on the large carnivore taxa commonly found at early hominin sites (i.e., hyaenids and felids). Modern African canids are cursorial, open-habitat adapted taxa. The relative scarcity of canid fossils in the African record may be a taphonomic bias, as open habitats are relatively under represented for much of the Plio-Pleistocene (Werdelin and Peigné 2010). Further, modern African hunting dogs have extremely large ranges that may stretch 1500-2000 km^2 (Estes and Goddard 1967; Nowak 1999). Their rarity in the fossil record may also be a function of their large range size. Because lycaon-like large canids were present during the Early Pleistocene of Africa, the subsequent gap in their fossil record may simply represent a preservation bias and not a true absence of large canids from paleolandscapes. Identification of their feeding signatures in the fossil record could provide important behavioral information regarding their possible competitive interactions with early hominins in Africa in light of possible taphonomic biases in the canid fossil record.

The relatively few studies of large canid bone modification patterns have examined frequencies of gnawing damage in archaeological assemblages modified by wolves (Stiner 2004), patterns of gross bone damage in experimental canid-modified assemblages (Binford

1981; Haynes 1982; Castel 2004) and biochemical modification of bone digested by wolves (Klippel et al. 1987; Esteban-Nadal et al. 2010). The most detailed study to date has been conducted by Campmas and Beuval (2008) who reported on gross bone modification and tooth pit dimensions produced by captive wolves on large ungulate carcasses. They concluded that overall damage patterns from captive wolves cannot be distinguished from that of wild hyenas, because captive wolves may engage in 'recreational gnawing' and so may damage bones more intensively than wild populations. Gnawing patterns produced by free ranging large canids have so far not been examined in detail.

Models for large canid tooth marking and bone breakage patterns on the scale of those that have been developed by others for hyaenids and felids are currently lacking. The research presented here will provide a baseline model for bone modification and preservation patterns in a canid-modified assemblage, as well as the largest taphonomic dataset of bones modified in large carnivore feeding experiments.

MATERIALS: CARNIVORE FEEDING EXPERIMENTS

Feeding experiments were conducted with captive wolf populations at the Wolf Conservation Center (WCC) in South Salem, New York (Hodgson et al. 2009, 2010). The wolves are housed in one-acre enclosures constructed simply by fencing in areas of woodland to keep their environs as natural as possible. They are fed a whole deer carcass diet on a schedule that approximates the feeding schedule of wild wolves (i.e., several times a week, not every day), and they have minimal contact with humans. Many of these wolves are being prepared for release into the wild. I believe my study animals represent an appropriate analog for wild wolves and are unlikely to show the tooth mark frequency discrepancies noted between wild and captive carnivores elsewhere (Gidna et al. 2013).

I studied bone assemblages produced by three different groups of wolves, with the following group composition:

Group 1: Mated pair of Red Wolves (*Canis rufus*) (weight range 53-78 lbs.)
Group 2: Mexican Gray Wolf pack (*Canis lupus baileyi*) composed of 15 individuals (weight range 59-80 lbs.)
Group 3: Pair of Mexican Gray Wolf female siblings (weight range 58-66 lbs.)

Variation in group size provides some information on damage produced under different competitive regimes. As part of normal wolf provisioning protocol at WCC, complete deer carcasses were fed to wolf groups (Fig. 1.2). Carcasses were obtained as road kill after WCC staff were alerted by the New York Department of Transportation. All carcasses fall within the bovid size class 2 category of Bunn (1982). A smaller sample of size class 3 bison limbs donated by a local farm was also included in the study. Wolf pairs were fed one carcass at a time, while the large group was fed 3 to 4 carcasses at a time, so there were fewer wolves per carcass in the large group, and thus higher competition. As the wolves could not be disturbed frequently, bones were collected as part of the normal maintenance of their enclosures every three months. This was carried out through systematic surface collection, which could not include sieving due to time constraints. Very small bone fragments were probably missed by this collection protocol, but small fragments are generally difficult to identify to anatomical part and so would not have been included in the GIS analysis. Bones that wolves may have swallowed,

INTRODUCTION

Arguably one of the major adaptive changes in hominin dietary evolution is the shift to increased consumption of animal tissue (including muscle, viscera, brains, and marrow). Meat eating by hominins is evidenced at Plio-Pleistocene archaeological sites in East Africa by butchery marks on bones of large mammals (Bunn 1981; Potts and Shipman 1981; Bunn 1983a; Bunn and Kroll 1986; the Plio-Pleistocene boundary is considered here to be 2.58 Ma following Gibbard et al. 2010). The earliest clear evidence for butchery is contemporaneous with the advent of the Oldowan stone tool industry at approximately 2.6 Ma, indicating that butchery was a component of the Oldowan as soon as tools appear (Semaw et al. 2003; Plummer 2004). The earliest evidence of cut marked bone associated with stone tools comes from Gona, Ethiopia (ca. 2.6 Ma) (Semaw et al. 2003) and the nearby locality of Bouri, Ethiopia (2.5 Ma) (de Heinzelin et al. 1999). More controversial evidence for cut marked bone which is not associated with stone tools dates to much earlier at ca. 3.4 Ma from Dikika, Ethiopia (McPherron et al. 2010). However, Domínguez-Rodrigo et al. (2010) have argued that the unclear taphonomic history of the Dikika finds call the authenticity of the reported cut marks into question, and that the marks may be trampling marks.

It has been traditionally assumed that *Homo habilis* was the maker of the Oldowan stone tools. In fact, this species name is taken from the Latin meaning "handy man" (Leakey et al. 1964). However, the earliest fossil evidence attributed to *Homo* dates to 2.33 Ma (the A.L. 666 maxilla from Hadar, Ethiopia) - nearly 300,000 years after the earliest stone tools are found (Kimbel et al. 1996). Plummer (2004) has suggested this means that either the antiquity of *Homo* has been underestimated or that an australopith on the lineage to *Homo* was the maker of the earliest Oldowan tools. The temporal range of the Oldowan (ca. 2.6-1.6 Ma) overlaps with three hominin genera: *Australopithecus*, *Paranthropus*, and *Homo* (Plummer 2004). The 2.5 Ma cut marked bones from Bouri are stratigraphically associated with *Australopithecus gahri* (Asfaw et al. 1999; de Heinzelin et al. 1999), and this has led some to suggest *A. gahri* was the first tool maker (Semaw et al. 2003). *Paranthropus* also overlaps Oldowan archaeological occurrences in both East and South Africa, and is found in the same archaeological level at Olduvai Gorge (FLK I, Level 22) with butchered bone as well as remains of *Homo habilis* (Leakey 1971). While the number of species making early stone tools is unclear, it is generally agreed that *Homo habilis* and early African *Homo erectus* (=*ergaster*) made Oldowan tools (Plummer 2004; but see Susman 1991). *Homo erectus*, known from 1.8 Ma, is clearly associated with stone tools (Isaac 1997; Anton 2003). *Homo habilis* is recognized now by most to encompass two species: a large, megadont form (*Homo rudolfensis*) and a more gracile form (*Homo habilis* sensu stricto) (Chamberlain 1989; Wood 1992). Because the ancestor of *Homo erectus* almost certainly would have used stone tools, evidence for an ancestor-descendant relationship between *Homo habilis* sensu stricto and *Homo erectus* (Strait et. al 1997) strongly suggests *H. habilis* sensu stricto was a tool maker. *H. habilis* sensu stricto was probably responsible for forming archaeological assemblages beginning around 2.3 Ma, while both *H. habilis* sensu stricto and *H. erectus* formed sites during the period in which they temporally overlap beginning at 1.8 Ma when *H. erectus* appears (Plummer 2004; Plummer et al. 2009b). As taxonomic attribution for the makers of the Oldowan is difficult to assign and because it is likely that multiple species of tool-makers existed during the Plio-Pleistocene, I will refer to them here as Oldowan hominins, with the assumption that the ca. 2 Ma tool-makers at FLK Zinj and Kanjera South were early members of the genus *Homo*.

Some important morphological changes took place in the hominin lineage with the transition from an *Australopithecus*-grade hominin to *Homo erectus*. These include an increase in body size, an increase in brain size and a shift toward dedicated bipedalism. These changes suggest an increased energy requirement for early members of the genus *Homo* (Aiello and Wheeler 1995; Aiello and Wells 2002; Leonard and Robertson 1994; Leonard et al. 2003). Increased energy expenditure would have required a higher quality diet. As a nutritionally dense food source, animal tissue may have been a key resource supporting increased nutritional requirements (Milton 1999; Aiello and Wells 2002). It is assumed that like other primates, hominins also consumed plant foods including fruits, seeds, nuts and plant underground storage organs. An increased consumption of animal tissue would have been a supplement to these plant foods (Plummer 2004). Meat comprises approximately one third to one half of the mean annual caloric intake in modern African hunter gatherer groups (e.g., Lee and DeVore 1968; O'Connell et al. 2002). Meat probably comprised less of the diet of early *Homo*, but it was likely a key source of protein and fat, and may have been a critical resource during times of seasonal plant food shortages (Foley 1987).

Evolutionary changes in the hominin lineage in the Late Pliocene are thought to have been spurred by environmental changes between 2.0-3.0 Ma. The onset of glaciation in the northern hemisphere during this time resulted in a cooling and drying trend in Africa, which ultimately led to an increase in grasslands relative to forest habitats, and likely resulted in an increase in overall habitat heterogeneity (deMenocal 1995; Cerling 1992; Bobe et al. 2002; Wynn 2004; Bobe 2006; Potts 2012; Magill et al. 2013). The decrease in forest habitats at this time would have resulted in a decrease in the availability of fruits and nuts which were probably main components of the australopith diet (Sept 1986; Foley 1987). This likely increased competition among hominins over forest-derived plant foods. Competition may have been further exacerbated by an increase in rainfall seasonality, which in modern African settings is associated with plant food shortages during dry seasons (Foley 1987). The proportional increase in grassland habitats beginning in the Late Pliocene would have provided few plant food resources for hominins, but grasslands do support large populations of grazing ungulates (Wynn 2004), and archaeological evidence shows that hominins had begun to exploit these new food sources by the Early Pleistocene.

It is well established that Oldowan hominins were at times butchering large mammal carcasses. However, the method of carcass acquisition (i.e., hunting vs. scavenging), the timing of access to carcass resources, the degree of carcass completeness (fleshed vs. defleshed) at the time of hominin access, as well as the importance of meat in the diet of Oldowan hominins is less certain. Research on this topic has revolved around a central debate over hunting versus scavenging (Binford 1985; Potts 1988; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003). Opinions regarding this debate vary widely from envisioning hominins as marginal scavengers of flesh scraps and within-bone resources left on carcasses of carnivore kills (Binford 1981, 1986, 1988; Shipman 1986; Blumenschine 1987, 1995; Blumenschine and Cavallo 1992; Capaldo 1995, 1997; Selvaggio 1994b, 1998; Pante et al. 2012) to aggressive scavengers of large mammal carcasses and possibly hunters of small mammals (Bunn and Kroll 1986; Potts 1988; Bunn and Ezzo 1993; Oliver 1994; Domínguez-Rodrigo 2002, 2009; Plummer 2004; Domínguez-Rodrigo et al. 2007; Ferraro et al. 2013).

The hunting-versus-scavenging debate has important implications for understanding the evolution of the genus *Homo*, not only in terms of diet, but also in terms of behavior (Domínguez-Rodrigo et al. 2007). Animal tissue is not only a potentially nutritionally important resource, but also a socially important one. Evidence for early carcass access could imply regular meat eating and instances of food surplus, which may have promoted food sharing or other cooperative behaviors that are important in modern human groups (Isaac 1978; Kaplan and Hill 1985; Hawkes et al. 2001; Marlowe 2001). Evidence for late carcass access would imply a more passive scavenging strategy, suggesting hominins were low ranking within the group of animals consuming large mammalian prey (Blumenschine 1995), and the social implications above may not apply (O'Connell et al. 2002). Given this, reconstructions of the potential amount of meat in the hominin diet and its method of acquisition have implications for interpreting hominin dietary as well as social evolution.

When hominins first began to encroach on the carnivore guild, they would not have been top predators, but gradually would have had to evolve strategies to survive in their new competitive environment (Lewis and Werdelin 2007). Brantingham (1998) has argued that hominin competition with carnivores for shared limited resources (i.e., large mammalian carcasses) led to coevolution in the form of resource partitioning and competition-driven character displacement. He argued that the advent of stone tool technology acted as a form of character displacement eventually allowing hominins to enter a centrally-positioned niche within the predatory guild.

It has long been argued that the increase in meat eating and concurrent increase in brain size allowed for an increase in social complexity in early hominins. This idea was first explicitly articulated in Lee and DeVore's (1968) *Man the Hunter* volume which resulted from a conference held in Chicago in 1966. Papers in this volume presented ethnographic evidence to support a claim that hunting has been an integral part of the evolution of modern human behavior. The hunting paradigm held sway in the field of paleoanthropology for more than a decade before being seriously questioned by researchers focused on the use of experimental methods and work grounded in archaeological rather than ethnographic evidence (Binford 1981; Brain 1981). Isaac's (1971, 1978) influential "home base" hypothesis argued that cooperation related to food acquisition may have been more important in shaping modern human behavior than the aggressive behaviors related to hunting that the "man the hunter" hypothesis focused on. The "home base" hypothesis argued that hominins would have used a base camp or central place from which they dispersed and returned to on a daily basis. According Isaac, the use of a home base would have entailed a sexual division of labor in which males hunted or scavenged and females gathered plant foods. These foods would have then been brought back to the home base to be shared.

In a subsequent hypothesis of Oldowan site formation, Schick (1987) argued that large sites where dense accumulations of stone tools and bones are found represent repeatedly-visited rich foraging areas where hominins had easy access to stone raw material. If raw material was readily available nearby, transport costs could have been lessened by discarding lithics at the site where bone refuse and stone tools would have accumulated over time. Schick argued that smaller sites may represent just a few behavioral events, or may represent areas were stone raw material was less common, so artifacts were transported away rather than being discarded on site. Bunn (1991) has argued for a similar "favored place" scenario to explain Oldowan site formation, where he envisioned these sites as repeatedly visited safe areas where hominins could rest, socialize, consume transported carcass parts, and make tools. Other models have argued Oldowan zooarchaeological sites represent places where hominins were able to take refuge and defend their resources from carnivores or other groups of hominins (Rose and Marshall 1996; Blumenschine 1987, 1991), or caches of stone raw material where carcasses were brought for processing (Potts 1984, 1991). These subsequent models did not assume food sharing or sexual division of labor as in Isaac's home base model. However, Oliver (1994) has argued that repeated use of sites as a predator avoidance strategy by hominins with altricial young would have provided a selective context for the development of food transport, provisioning, and food-sharing behaviors in hominins. Presently, there is still little agreement among researchers on the nature and function of Oldowan hominin archaeological sites. As such, answering questions about the mode of hominin carcass acquisition at these sites has direct bearing on our ability to understand other aspects of hominin socioecology.

In this dissertation I examine the issue of hominin meat acquisition through an analysis of carnivore- and hominin-induced damage on the approximately 2 Ma archaeofaunal assemblage from Kanjera South, Kenya and the slightly younger assemblage from FLK I Level 22 (FLK Zinj), Olduvai Gorge, Tanzania. I analyze these assemblages using an experimental framework of new and existing taphonomic models replicating how carnivores and humans damage bone. The following provides a summary of the structure of this dissertation.

In Chapters 1 and 2, I report on new experimental research on bone modification patterns and tooth mark frequencies produced by large canids (multiple species of wolves) and large felids (lions and tigers). This work adds to the growing body of neotaphonomic literature on carnivore bone modification by providing the largest experimental assemblage of bones modified by these taxa to date. Neotaphonomic is defined here following Hill (1978) to include experimental observations of modern processes of bone decay and deposition designed to test interpretations of the fossil record. I use a GIS image analysis approach to characterize bone damage patterns (including bone surface damage and fragmentation) in the experimental assemblages in this study. This research presents the first application of GIS image analysis to study patterns of carnivore bone modification. I expand on the method originally described by Marean and colleagues (Nilssen 2000; Marean et al. 2001; Abe et al. 2002) by incorporating use of the ArcGIS Spatial Analyst tools to identify areas of significantly dense tooth marking across elements. In addition to the neotaphonomic assemblages of carnivore bone modification that I present here, I use GIS image analysis to characterize damage patterns observed in Blumenschine's (1995) previously studied experimental bone assemblages which model differing scenarios of carnivore-only, hominin-only and hominin-first access to carcasses.

In the second part of this dissertation, I use the framework of GIS experimental models I have created to interpret bone modification patterning in the Kanjera South (Chapter 3) and FLK Zinj (Chapter 4) archaeofaunal assemblages. The aim of this aspect of my research is to address questions about the order of access by hominins and carnivores to carcass resources at these sites in order evaluate Oldowan hominin foraging ecology and competitive interactions with carnivores. My results indicate that at Kanjera South, the pattern of bone preservation for small and medium bovids (size 1-3a, following Bunn 1982) is similar to GIS-generated models based on experimental bone assemblages that were first butchered and hammerstone fractured by humans, and subsequently scavenged by carnivores. The distribution of bone modifications on the Kanjera fauna revealed in the GIS analysis also suggests hominins had early access to small and medium bovids. Large bovids are not as well represented at Kanjera, and so bone damage patterns are difficult to characterize, but evidence presented here suggests hominins may have been scavenging the larger bovids. These results lend further support to the interpretation of early access of size 1 and 2 bovids that has been made for this site by Ferraro et al. (2013).

The interpretation of the nature of hominin involvement in the well-studied archaeofaunal assemblage from FLK Zinj has been a subject of some disagreement in the literature (Bunn 1986; Blumenschine 1995; Oliver 1994; Selvaggio 1994b, 1998; Capaldo 1997; Dominguez-Rodrigo and Barba 2006; Dominguez-Rodrigo et al. 2007; Blumenschine et al. 2007; Pante et al. 2012). The new GIS image analysis data I present here for the FLK Zinj assemblage suggest early access by hominins to fleshed carcasses at FLK Zinj, particularly of smaller prey, which may have been acquired through hunting. Damage patterns on larger carcasses are more difficult to interpret, but are not inconsistent with early access (hunting or aggressive scavenging). Further, a reanalysis of carnivore tooth mark frequencies in the FLK Zinj assemblage corroborate those cited by Domínguez-Rodrigo and colleagues (2007), lending additional support to an early access scenario for hominins.

CHAPTER 1. A GIS-Based Approach to Documenting Large Canid Damage to Bones

ABSTRACT

Experimental studies of modern carnivore tooth marking patterns are integral to understanding the nature of carnivore involvement in archaeological bone assemblages. However, modern bone damage data for most carnivore taxa are limited. This is particularly true for canids. Here I present bone damage data collected from feeding experiments conducted with Mexican Gray Wolves (*Canis lupus baileyi*) and Red Wolves (*Canis rufus*). This is the largest experimental assemblage reported for canids to date. I use the GIS image analysis approach described by Marean et al. (2001) to document bone preservation and tooth mark distribution, which is the first application of this approach to a carnivore-modified bone assemblage. Further, I introduce the use of the ArcGIS Spatial Analyst to identify significant concentrations of bone modifications. My results show the distribution of tooth pits varies considerably across elements as well as across different portions of the same element, and that significant clusters of tooth pits occur on all long bones. My results suggest that with a large enough sample, the GIS Spatial Analyst can be a useful tool for analyzing the distribution of bone modifications with greater resolution than previous methods. This method facilitates comparisons between experimental and fossil assemblages which may aid in identifying the timing of access to carcasses by carnivores involved in modifying fossil assemblages. Finally, the use of this rigorous methodology is a step toward increasing standardization in methods of taphonomic analysis.

INTRODUCTION

Bone damage patterns created on prey animals by modern carnivores can be used as a proxy to interpret the involvement of extinct carnivores in archaeological bone assemblages. This question has been particularly pertinent to researchers interested not only in carnivore behavior, but also in assessing potential competitive interactions between carnivores and hominins over the course of human evolution. Unfortunately, modern experimental datasets for carnivore-induced modifications are limited. This is particularly true for canids, which were potentially important agents of bone modification and assemblage formation during the Plio-Pleistocene of Eurasia, North America and Africa.

Taphonomic studies of carnivore bone modification have paid particular attention to patterns produced by hyaenids (Blumenschine 1988; Marean and Spencer 1991; Marean et al. 1992; Blumenschine and Marean 1993; Capaldo 1997; Faith 2007; Kuhn et al. 2009) and felids (Domínguez-Rodrigo 1999; Domínguez-Rodrigo and Barba 2006; Pobiner 2007; Gidna et al. 2013) in African settings. However, little attention has been paid to the bone modification signature of large canids. Canids were an important part of the Pleistocene large carnivoran paleoguild, and some were potentially high-level competitors (Brugal and Boudadi-Maligne 2011). Although large canid fossils overlap with modern and pre-modern human archaeological occurrences, the degree to which large canids may have competed with and influenced food acquisition behaviors of pre-modern humans is not well understood.

This study presents new bone damage data from feeding experiments conducted with large canids. I use a GIS image analysis method to record and analyze bone preservation patterns and surface modifications in this assemblage. This method, developed by Marean et al. (2001), provides a powerful means of analyzing and archiving large amounts of bone fragment data. Using the GIS image analysis method has several advantages. 1) It allows for more accurate recording and better visual representation of bone surface modifications, which can be examined relative to the degree of preservation of particular element portions. 2) The powerful relational database function of ArcGIS software provides a means of organizing and analyzing data on a finer scale than would otherwise be possible, including damage density and the spatial relationship of damage to anatomical markers. 3) This approach can provide a means of standardizing zooarchaeological data collection methods.

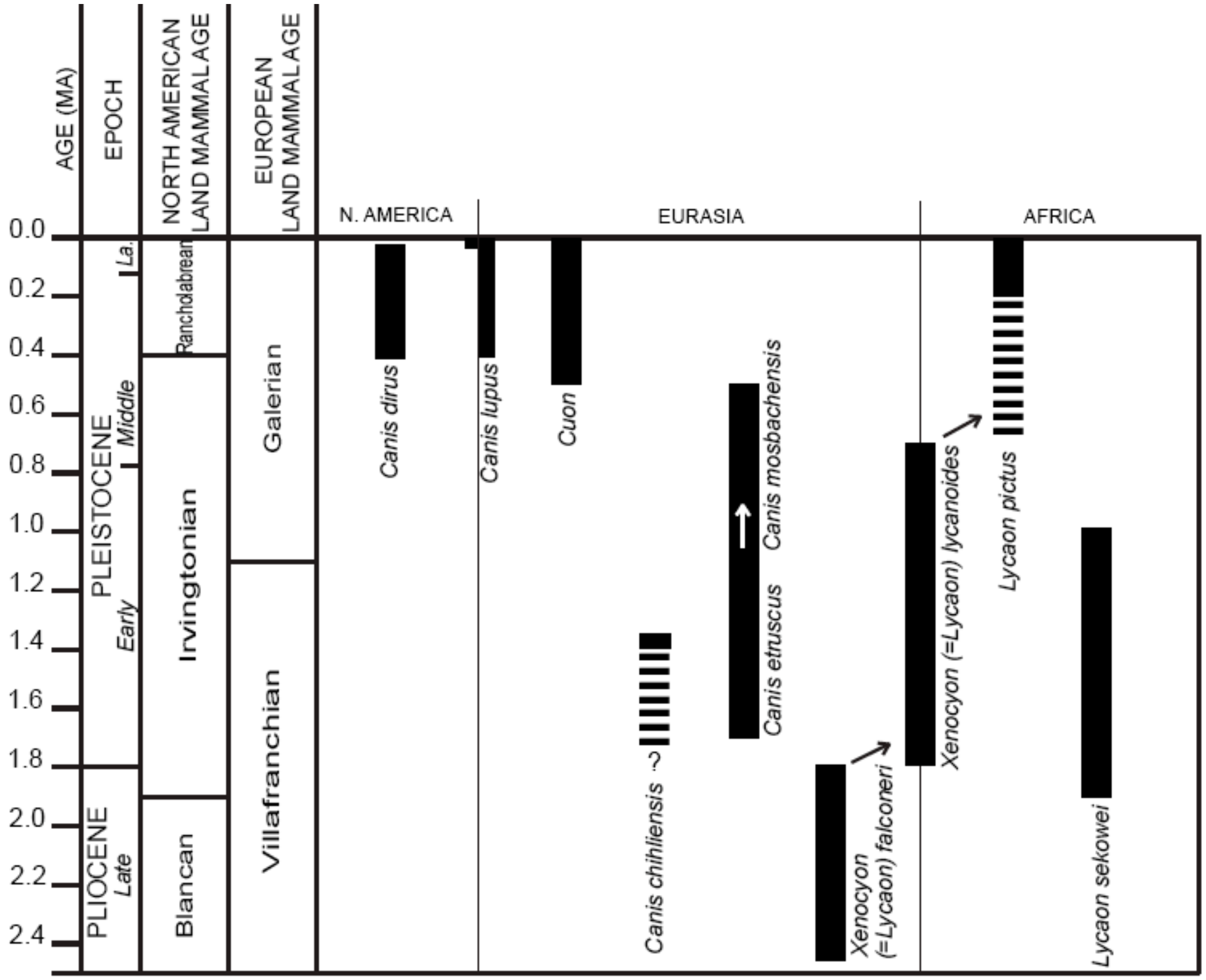
Pleistocene Large Canid Distribution

Canids are abundant and taxonomically diverse throughout the Plio-Pleistocene record of Europe (Brugal and Boudadi-Maligne 2011). Large canids appear in the Western European record just below the Plio-Pleistocene boundary at around 2 Ma (this is the original boundary designation prior to the recent revision by Gibbard et al. 2010), following the well known European faunal turnover 'wolf-event' (Azzaroli 1983; Torre et al. 1992). This turnover is marked by a major extinction of carnivores in Europe, including the cursorial hyaenid *Chasmaporthetes lunensis*, the appearance of the large hyaenid *Pachycrocuta brevirostris,* and a radiation of large canid species (Martínez-Navarro and Rook 2003; Sardella and Palombo 2007).

Some of the earliest canids in Europe that potentially overlap pre-modern humans are the wolf-like *Canis etruscus* and *Canis mosbachensis* (Fig. 1.1). Although their taxonomy is disputed, these species are potentially a single lineage that persisted from the Early through the Middle Pleistocene. The modern *Canis lupus* lineage appears in the Late Pleistocene (Brugal and Boudadi-Maligne 2011). Dental morphometric analyses show that the slicing component of the *C. lupus* dentition is more developed than the crushing component, suggesting that wolves have a more carnivorous diet than these earlier species of *Canis* (Brugal and Boudadi-Maligne 2011).

Two other genera of large, hyper-carnivorous (flesh specialist) canids are present in Pleistocene Eurasia: *Cuon* (the Asiatic wild dog) and *Xenocyon*, which some consider to be the same genus as the African hunting dog *Lycaon* (Martínez-Navarro and Rook 2003). The genus *Xenocyon* includes two chronospecies - *Xenocyon* (=*Lycaon*) *falconeri* and *Xenocyon* (=*Lycaon*) *lyconoides* - which persisted in Eurasia until the Middle Pleistocene (Martínez-Navarro and Rook 2003). These earlier species of lycaon-like canids were larger in size than extant African

Figure 1.1. Distribution of large canid species during the Late Pliocene and Pleistocene.



Arrows indicate chronospecies. Dotted line indicates insecure record. Age ranges for species based on the following: C. dirus (Dundas 1999); C. lupus, Cuon, C. etruscus, C. mosbachensis (Brugal & Boudadi-Maligne 2011); C. chihliensis (Tong et al. 2012); X. falconeri; X. lycanoides, L. pictus (Martínez-Navarro & Rook 2003); L. sekowei (Hartsone-Rose et al. 2010)

hunting dogs and more comparable to modern wolves, with hyper-carnivorous dental morphology (Martínez-Navarro and Rook 2003).

The African fossil record of canids is comparatively small. The earliest larger-sized canids (i.e., larger than jackal-sized) from Africa are known at Ain Hanech, Algeria (1.8 Ma) (Sahnouni et al. 2002), and also from Kromdraai Member A (ca. 1.5 Ma) (Turner 1986; Geraads 2011), Sterkfontein Valley Coopers D (1.6-1.9 Ma) and Gladysvale (1.0 Ma) (Hartstone-Rose et al. 2010), and Olduvai Beds I (ca. 1.84) and II (ca. 1.75-1.20) (Ewer 1965). These African species have been published under various names (*Canis atrox, Canis africanus*), but they likely represent the same species (Geraads 2011). Martínez-Navarro and Rook (2003) have synonymized *Canis africanus* with Eurasian *Xenocyon lycanoides* as a plausible ancestor for modern *Lycaon*. The modern African hunting dog (*Lycaon pictus*) is smaller in size than these fossil species and relatively recent in origin (Werdelin and Lewis 2005). Although larger in size, the earlier Pleistocene forms in Africa display a dental morphological pattern suggestive of less hyper-carnivory than modern *L. pictus* (Martínez-Navarro and Rook 2003).

The North American large canid fossil record is much better known than the African record. The dire wolf (*Canis dirus*) was one of the most common mammalian species during the Rancholabrean Land Mammal Age of North America (Middle to Late Pleistocene) and has been reported from 136 localities (Dundas 1999). The dire wolf was similar in size to *Canis lupus*, but more heavily built, and with a significantly more robust dentition (Kurtén and Anderson 1980). There has been some debate over the feeding behavior of this species. Some have suggested *C. dirus* was capable of crushing bone and may have filled a hyena-like scavenging niche in North America (Biknevicius and Ruff 1992). Others, however, have argued that although larger in size, the craniofacial and dental morphology closely mirror *C. lupus*, suggesting a wolf-like hunting and feeding behavior (Anyonge and Baker 2006). *Canis dirus* was among the taxa that succumbed to the megafaunal extinction at the end of the Pleistocene. Modern *Canis lupus*, which arose in the Old World, is not seen in North America until the Late Pleistocene, but is one of the most widely distributed land mammals after that time. Its historic distribution covered the majority of the Northern hemisphere, stretching from the Arctic through northern Mexico, as well as in Eurasia and North Africa (Kurtén and Anderson 1980; Feldhamer et al. 2003; Gaubert et al. 2012).

Canids as Potential Bone Modifying Agents, and Taphonomic Research to Date

The above overview shows that large canids were present during and overlapping periods of human occupation at points of critical interest in human evolutionary history, and thus were potentially important contributors to or modifiers of the Pleistocene zooarchaeological record. In part, the paucity of taphonomic research on large canids is due to their underrepresentation at African sites relative to other large carnivore species. Much of the research on carnivore bone modification has been conducted in African contexts with the aim of answering questions regarding the origins of hominin meat-eating behaviors, and so has focused on the large carnivore taxa commonly found at early hominin sites (i.e., hyaenids and felids). Modern African canids are cursorial, open-habitat adapted taxa. The relative scarcity of canid fossils in the African record may be a taphonomic bias, as open habitats are relatively under represented for much of the Plio-Pleistocene (Werdelin and Peigné 2010). Further, modern African hunting dogs have extremely large ranges that may stretch 1500-2000 km^2 (Estes and Goddard 1967; Nowak 1999). Their rarity in the fossil record may also be a function of their large range size. Because lycaon-like large canids were present during the Early Pleistocene of Africa, the subsequent gap in their fossil record may simply represent a preservation bias and not a true absence of large canids from paleolandscapes. Identification of their feeding signatures in the fossil record could provide important behavioral information regarding their possible competitive interactions with early hominins in Africa in light of possible taphonomic biases in the canid fossil record.

The relatively few studies of large canid bone modification patterns have examined frequencies of gnawing damage in archaeological assemblages modified by wolves (Stiner 2004), patterns of gross bone damage in experimental canid-modified assemblages (Binford

1981; Haynes 1982; Castel 2004) and biochemical modification of bone digested by wolves (Klippel et al. 1987; Esteban-Nadal et al. 2010). The most detailed study to date has been conducted by Campmas and Beuval (2008) who reported on gross bone modification and tooth pit dimensions produced by captive wolves on large ungulate carcasses. They concluded that overall damage patterns from captive wolves cannot be distinguished from that of wild hyenas, because captive wolves may engage in 'recreational gnawing' and so may damage bones more intensively than wild populations. Gnawing patterns produced by free ranging large canids have so far not been examined in detail.

Models for large canid tooth marking and bone breakage patterns on the scale of those that have been developed by others for hyaenids and felids are currently lacking. The research presented here will provide a baseline model for bone modification and preservation patterns in a canid-modified assemblage, as well as the largest taphonomic dataset of bones modified in large carnivore feeding experiments.

MATERIALS: CARNIVORE FEEDING EXPERIMENTS

Feeding experiments were conducted with captive wolf populations at the Wolf Conservation Center (WCC) in South Salem, New York (Hodgson et al. 2009, 2010). The wolves are housed in one-acre enclosures constructed simply by fencing in areas of woodland to keep their environs as natural as possible. They are fed a whole deer carcass diet on a schedule that approximates the feeding schedule of wild wolves (i.e., several times a week, not every day), and they have minimal contact with humans. Many of these wolves are being prepared for release into the wild. I believe my study animals represent an appropriate analog for wild wolves and are unlikely to show the tooth mark frequency discrepancies noted between wild and captive carnivores elsewhere (Gidna et al. 2013).

I studied bone assemblages produced by three different groups of wolves, with the following group composition:

Group 1: Mated pair of Red Wolves (*Canis rufus*) (weight range 53-78 lbs.)
Group 2: Mexican Gray Wolf pack (*Canis lupus baileyi*) composed of 15 individuals (weight range 59-80 lbs.)
Group 3: Pair of Mexican Gray Wolf female siblings (weight range 58-66 lbs.)

Variation in group size provides some information on damage produced under different competitive regimes. As part of normal wolf provisioning protocol at WCC, complete deer carcasses were fed to wolf groups (Fig. 1.2). Carcasses were obtained as road kill after WCC staff were alerted by the New York Department of Transportation. All carcasses fall within the bovid size class 2 category of Bunn (1982). A smaller sample of size class 3 bison limbs donated by a local farm was also included in the study. Wolf pairs were fed one carcass at a time, while the large group was fed 3 to 4 carcasses at a time, so there were fewer wolves per carcass in the large group, and thus higher competition. As the wolves could not be disturbed frequently, bones were collected as part of the normal maintenance of their enclosures every three months. This was carried out through systematic surface collection, which could not include sieving due to time constraints. Very small bone fragments were probably missed by this collection protocol, but small fragments are generally difficult to identify to anatomical part and so would not have been included in the GIS analysis. Bones that wolves may have swallowed,

Figure 1.2. Mexican Gray Wolves at the Wolf Conservation Center during feeding experiments.

Photo credit: Spencer Wilhelm

digested, and deposited in scat were also not collected, as other research has shown that these are typically vertebral (Esteban-Nadal et al. 2001), and my focus here is on the limb bones. Because most bones had been exposed to the elements for at least several weeks, they were largely defleshed prior to collection. Bones were degreased and cleaned of any remaining tissue by boiling in a mild solution of water and laundry detergent in the Anthropology Bone Research Laboratory at Queens College. All bones in the sample were examined with a 10x hand lens under oblique light to identify tooth marks. Tooth marks were identified based on published criteria (Binford 1981; Bunn 1981; Blumenschine et al. 1996; Domínguez-Rodrigo and Barba 2006).

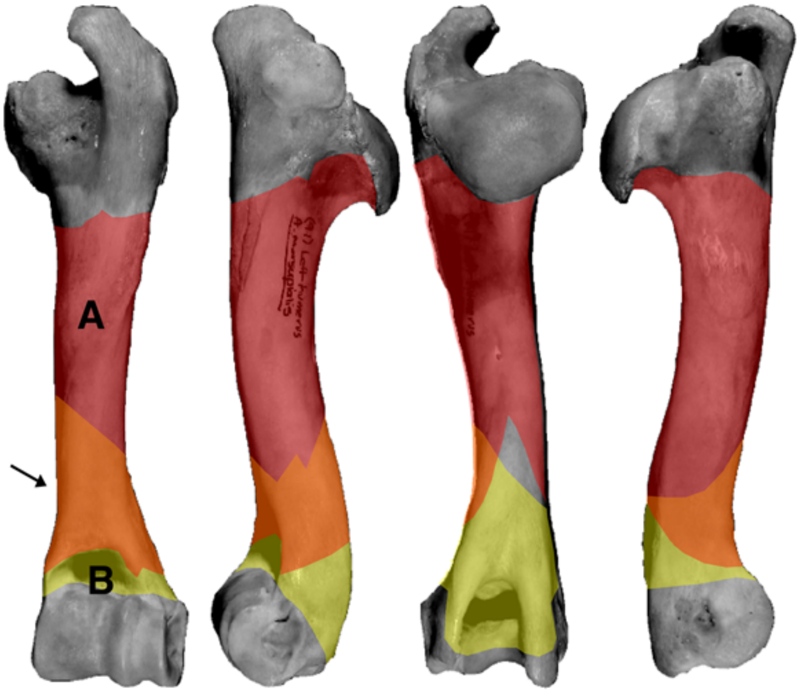
METHODS – GIS IMAGE ANALYSIS

I used a GIS image analysis approach to record bone preservation and tooth mark distribution in the assemblage. This method was originally developed for analysis of hominin-induced cut marks (Marean et al. 2001; Abe et al. 2002). However, it is well suited to documenting other types of bone modification as well. My study is the first to apply this approach to a carnivore-modified bone assemblage. The approach essentially treats each element as a "map" onto which the outline of bone fragments, as well as bone surface modifications are recorded.

Bone Portion Survivorship

This procedure utilizes ArcGIS software along with the Spatial Analyst extension and is fully described in Marean et al. (2001). Using this method, the outline of each identifiable fragment is digitally drawn as a vector image in ArcGIS over a photographic template of a complete bone. The photo template allows for accurate drawing of fragments relative to anatomical landmarks. Each fragment is drawn as a separate layer, which consists of a shape file linked to a table containing specific information about that fragment. The spatial coordinate system in ArcGIS allows a large number of fragment shape files to be superimposed over the element template, providing the basis for calculating the minimum number of elements (MNE). The maximum number of fragment overlaps indicates the MNE (Fig. 1.3). This process produces a shaded MNE "map" which is a composite digital record of the size, position, and shape of all identifiable fragments of a particular element and side, as well as an accurate visual representation of bone portion survivorship (Abe et al. 2002). Marean et al. (2001, supplementary material) have provided templates and several ArcView scripts that automate some of the data entry process. Data entry can also be accomplished without use of the scripts in more recent versions of ArcGIS.

Figure 1.3. GIS image analysis fragment entry. This image shows two sample fragments (A and B) from the left humerus that have been drawn on the GIS template. Areas of fragment overlap (indicated by the arrow) provide the basis for calculating the MNE.

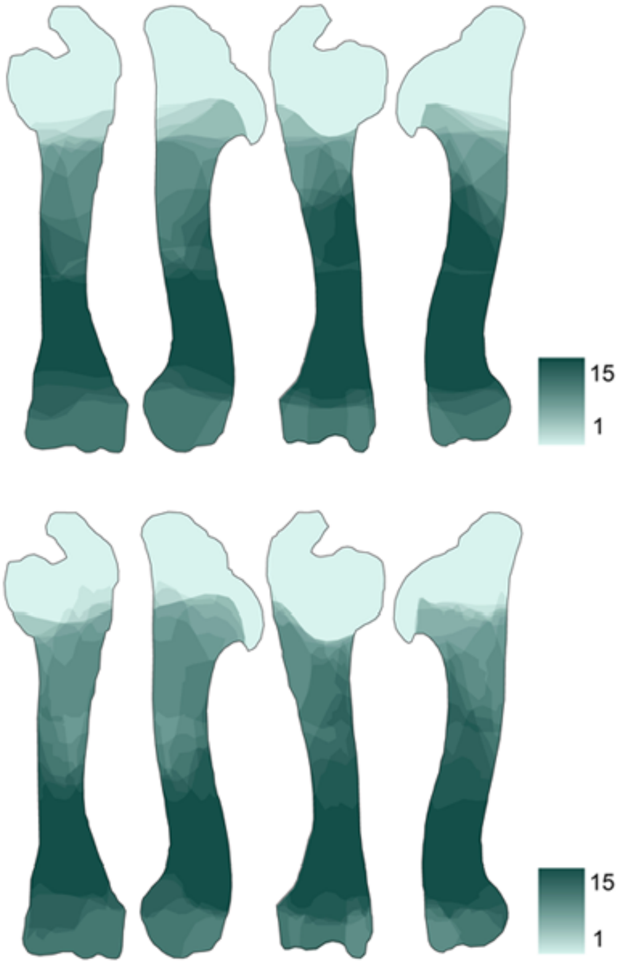


The MNE function in this software is useful for providing a visual representation of which bone portions are frequently deleted by carnivore consumption, and which portions are more often preserved. Lyman (2008) has argued that because this method calculates MNE by overlapping pixels in image files that are drawn by hand, it could potentially inflate MNE counts if fragments that do not overlap in reality are drawn slightly overlapping. He conducted a trial with a single student participant to test the replicability of fragment shape drawing and accuracy of MNE counts using an experimental bone assemblage of known derivation. The student in this study was able to fairly consistently reproduce the shape of fragments, but fragment size and location on the template varied from trial to trial. This resulted in MNE tallies that were 0-50 percent greater than the actual number.

I have conducted additional trials to test replicability of fragment drawing between observers, as well as MNE counts based on direct comparisons between specimens. I conducted a replicability study on a subset of the experimental bone assemblage along with a zooarchaeology student intern trained in the GIS image analysis method. My study also found that fragment shape was consistently reproduced, and MNE counts were consistent between participants. Both observers obtained an MNE of 15 (the actual MNE in the assemblage was 16), and the MNE map images appear almost indistinguishable (Fig. 1.4). This could be explained by the level of training in bone anatomy the participants in this study had received, relative to the student in Lyman's trial.

Although replicability in fragment drawing and MNE counts using the GIS system was consistent between observers in this study, MNE counts generated using GIS are slightly underestimated (on average by about 17%) compared with counts generated using the traditional overlap approach (as described in Marean et al. 2001). This is likely because skeletal age and other observable features that might indicate two fragments are actually from two separate individuals are not taken into account as they would be using the overlap approach. I argue the GIS method is best used in conjunction with hands-on examination and is not a substitute for fragment refitting. It does provide a rough minimum MNE and is particularly useful in large assemblages when it is not practical or possible to lay out a whole assemblage for comparative purposes. In my opinion, one of the most useful features of the MNE function is that it provides an informative visual display of the pattern of bone portion survivorship.

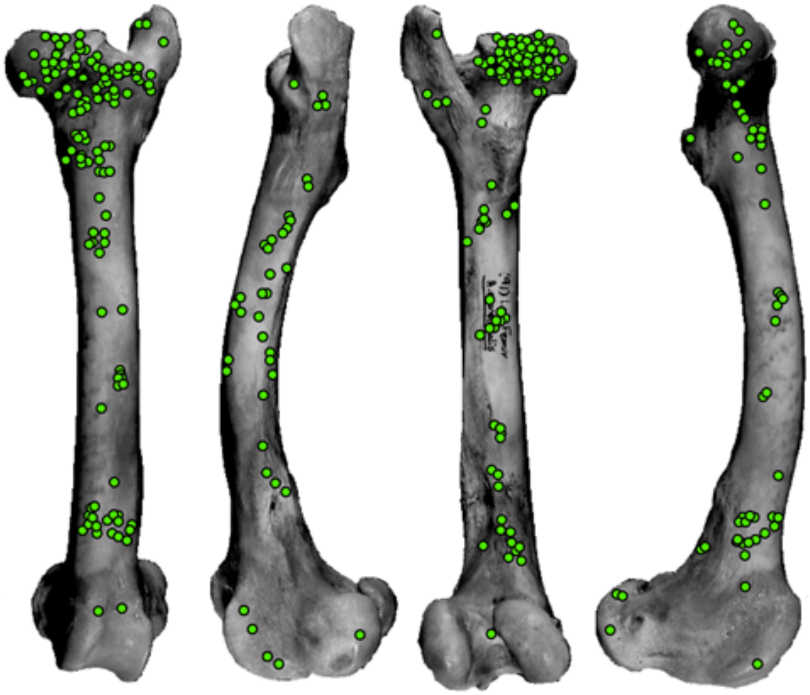
Figure 1.4. MNE replicability test. MNE maps were created independently by two researchers.



Cluster Analysis of Bone Surface Modifications

The GIS image analysis method also allows bone surface modifications to be spatially recorded on each element. Other researchers have used this method to document cut mark distribution (Nilssen 2000; Abe et al. 2002), and I have found it equally useful for documenting carnivore tooth mark distribution (Hodgson et al. 2009, 2010). The exact position of tooth marks by type (e.g., tooth pits, tooth scores, notches) is spatially plotted in a single layer file over a template of a complete bone, resulting in a composite record of the distribution of bone modifications for each element (Fig. 1.5). Further, each modification entry is linked to a database table containing specific information about the mark (e.g., specimen number the mark occurs on; tooth pit dimensions; pit type; pit location on cortical, medullary or fracture surface - any variable the researcher wishes to record can be entered here).

Figure 1.5. Example of a composite plot for tooth pits created by wolves on the femur.



Data analysis was conducted in ArcGIS 9.2 using the Spatial Analyst extension. I have expanded upon the method of analysis described by Marean et al. (2001), and make use of the improved ArcGIS spatial statistical tools now available. The Density and Analyzing Patterns toolsets within ArcGIS were used to analyze clustering patterns of bone modifications. The Average Nearest Neighbor Distance tool (Spatial Statistics → Analyzing Patterns) was used to measure the distance between individual tooth marks and to test for significant spatial clusters. If the average distance between points (tooth marks) is less than the average for a hypothetical random distribution, the distribution is considered clustered (ESRI 2011). I also used the Density tool (Kernel Density) to visually identify where clusters of modifications are most concentrated on specific elements. See supplemental material to this chapter for a detailed description of analysis steps.

RESULTS AND DISCUSSION

Bone Portion Survivorship Results

Figures 1.6 and 1.7 show results of the GIS-generated maps of bone portion survivorship for the long bones. These images represent a composite record of all fragments identifiable to side for each specific element. The maps are shaded according to which element portions are most typically preserved in the assemblage, with darker portions indicating areas of highest survivorship. Because these darkest areas represent locations where the highest number of fragments overlap, this number of overlaps provides an estimated MNE. Data from the large group of 15 Mexican Gray Wolves (Group 2) and the pair of Mexican Gray Wolves (Group 3) are displayed side by side to give an indication of variation in bone preservation that might be related to differences in group size during carcass feeding.

Figure 1.6. Bone preservation for forelimbs in small and large wolf group experiments. Dark shaded areas indicate areas of highest survivorship (highest number = MNE). Light areas indicate lowest survivorship. Small group = experiments conducted with wolf pairs. Large group = experiments conducted with group of 15 individuals. a. humerus, b. radius, c. ulna, d. metacarpal. There were no visible differences between right and left elements, so only the left side is shown. All bones are size class 2.

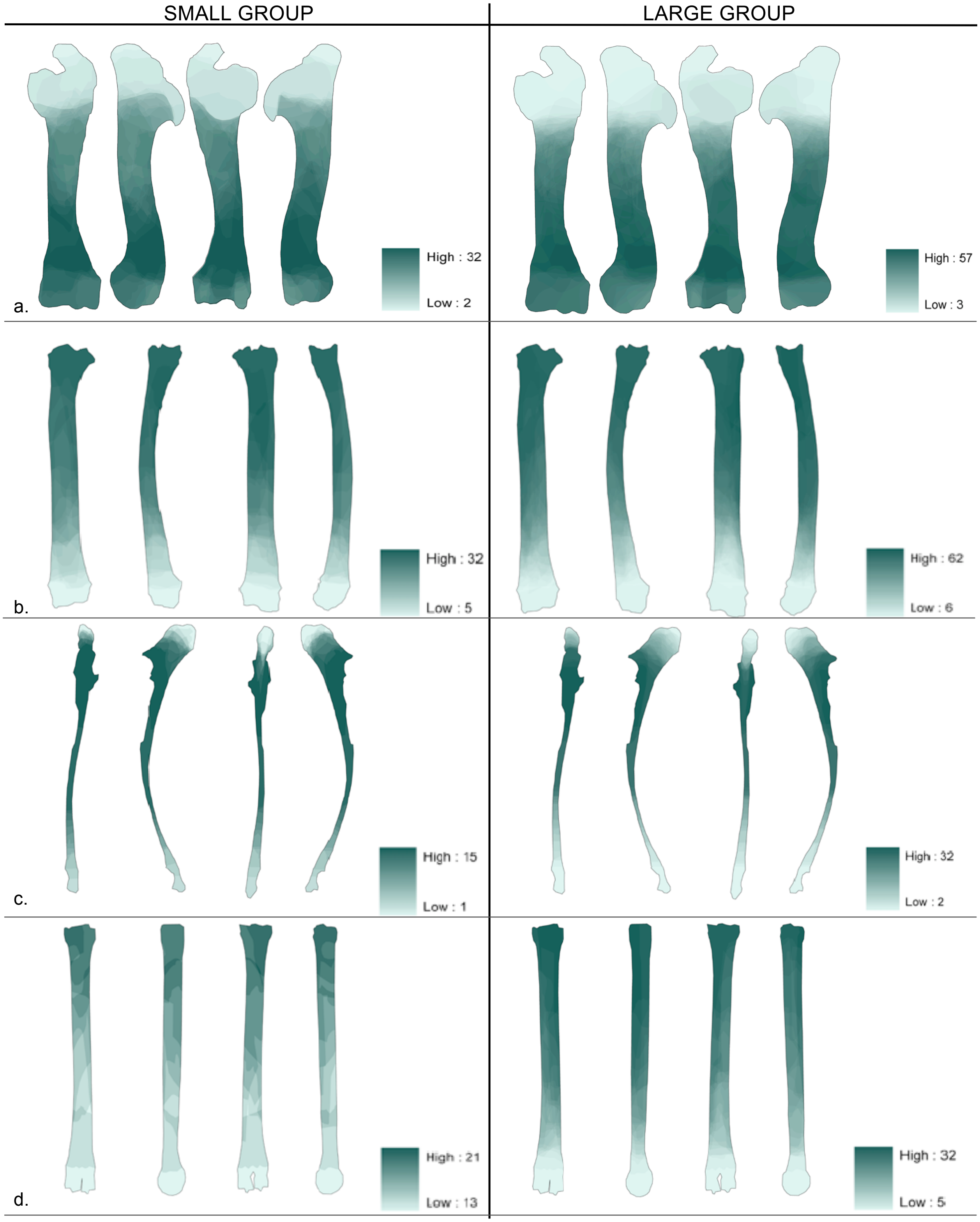
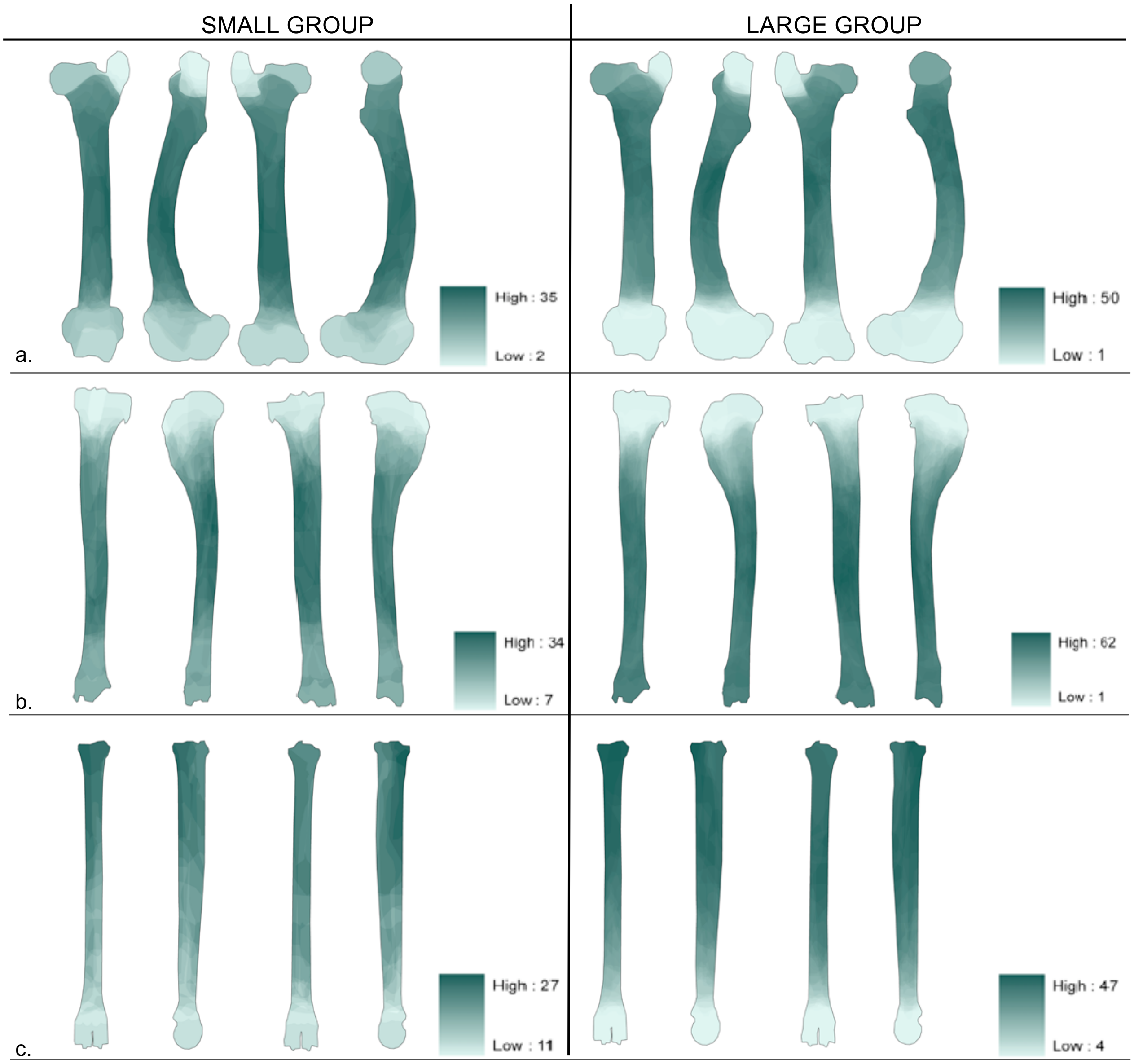


Figure 1.7. Bone preservation for hindlimbs in small and large wolf group experiments. Dark shaded areas indicate areas of highest survivorship (highest number = MNE). Light areas indicate lowest survivorship. Small group = experiments conducted with wolf pairs. Large group = experiments conducted with group of 15 individuals. a. femur, b. tibia, c. metatarsal. There were no visible differences between right and left elements, so only the left side is shown. All bones are size class 2.



The results show that many long bones are preserved as cylinders with destruction and consumption of one or both epiphyses being common. Differences between the small and large groups are simply differences in degree rather than kind. There is an increased potential for feeding competition in large groups, making it likely that carcasses will be more thoroughly consumed at an earlier stage, and thus exhibit more damage related to accessing the marrow cavity. The difference in damage degree between samples likely reflects different intensities of feeding competition within the large and small groups, though little work has been done on modeling variation in carnivore damage in high versus low competitive environments. The range of damage intensities seen in these samples likely represent a range of the variation one might expect to find on the damage continuum for large canids.

As a general pattern in these experiments, the grease-rich proximal humeral epiphysis is almost always consumed (Fig. 1.6), while the joint between the distal humerus and proximal radius and ulna is typically intact, save for the olecranon process of the ulna. In the hind limb (Fig. 1.7), the greater trochanter of the femur is typically removed, while the femoral head is preserved at more intermediate frequencies. The distal epiphysis of the femur is nearly always consumed. In only one out of 50 cases did the distal epiphysis survive wolf consumption in the large group experiment. As part of this joint, the proximal tibia is also nearly always consumed. Distal ends of metapodials are not well preserved, while the proximal ends normally remain.

I should also note that carnivore destruction of bone is known to be a density-mediated process. Carnivores tend to destroy the low-density and grease-rich cancellous portions of the epiphyses, while the more compact midshaft sections of the long bones have a higher potential for survival (Marean and Frey 1997). My models confirm this pattern, showing higher survivorship of midshaft sections relative to epiphyses.

Clustering of Tooth Marks

Figure 8 shows results of the GIS density analysis on bones modified by the large wolf group. This represents the higher end of the range of damage seen in these experiments. It is this high end of the range that is most informative for potentially distinguishing damage patterns produced by different carnivore taxa on prey of particular sizes, as multiple carnivore taxa may overlap in the low end of the range (Haynes 1983; Delaney-Rivera et al. 2009). Results show clusters of tooth pits on all long bone elements, but there is a great deal of variation in the distribution of these clusters across different elements.

Despite variation across bone elements, a cluster analysis (Table 1.1) shows that the distribution of tooth pits across long bones is non-random. Areas of significantly dense tooth pitting were identified on all aspects (i.e., anterior, posterior, medial, lateral) of the hind limb bones for both groups, and on at least two aspects of the other long bones, with clustering becoming more common in the large group experiments. As can be seen on the density analysis images (Fig. 1.8), the femoral head as well as the proximal diaphysis and distal end of the humerus display dense concentrations of tooth pits. The cluster on the proximal diaphysis of the humerus is just posterior to the deltoid tuberosity, and is likely associated with removal of the brachialis muscle. The proximal shaft of the tibia, distal shaft of the radius, and olecranon process of the ulna also have dense tooth mark concentrations. I found lower degrees of tooth marking on the femoral midshaft. The high degree of tooth marking seen on the metapodials was unexpected, given the relative lack of flesh on this element as well as the lower proportion of cancellous bone in the epiphyses. It should be noted that areas of extremely low preservation (as seen in Figs. 6 and 7) do not display clusters of tooth pits. This is due to their near total deletion from the assemblage. Importantly, these areas include the greater trochanter of the femur, proximal humerus, and the anterior tibial tuberosity.

Figure 1.8. GIS density analysis results of tooth pit distribution performed on composite tooth pit plots for each element in wolf experiments. Experiments shown here were conducted with the large wolf group. Red areas indicate highest concentrations of tooth pits. There were no visible differences between right and left elements, so only the left side is shown.

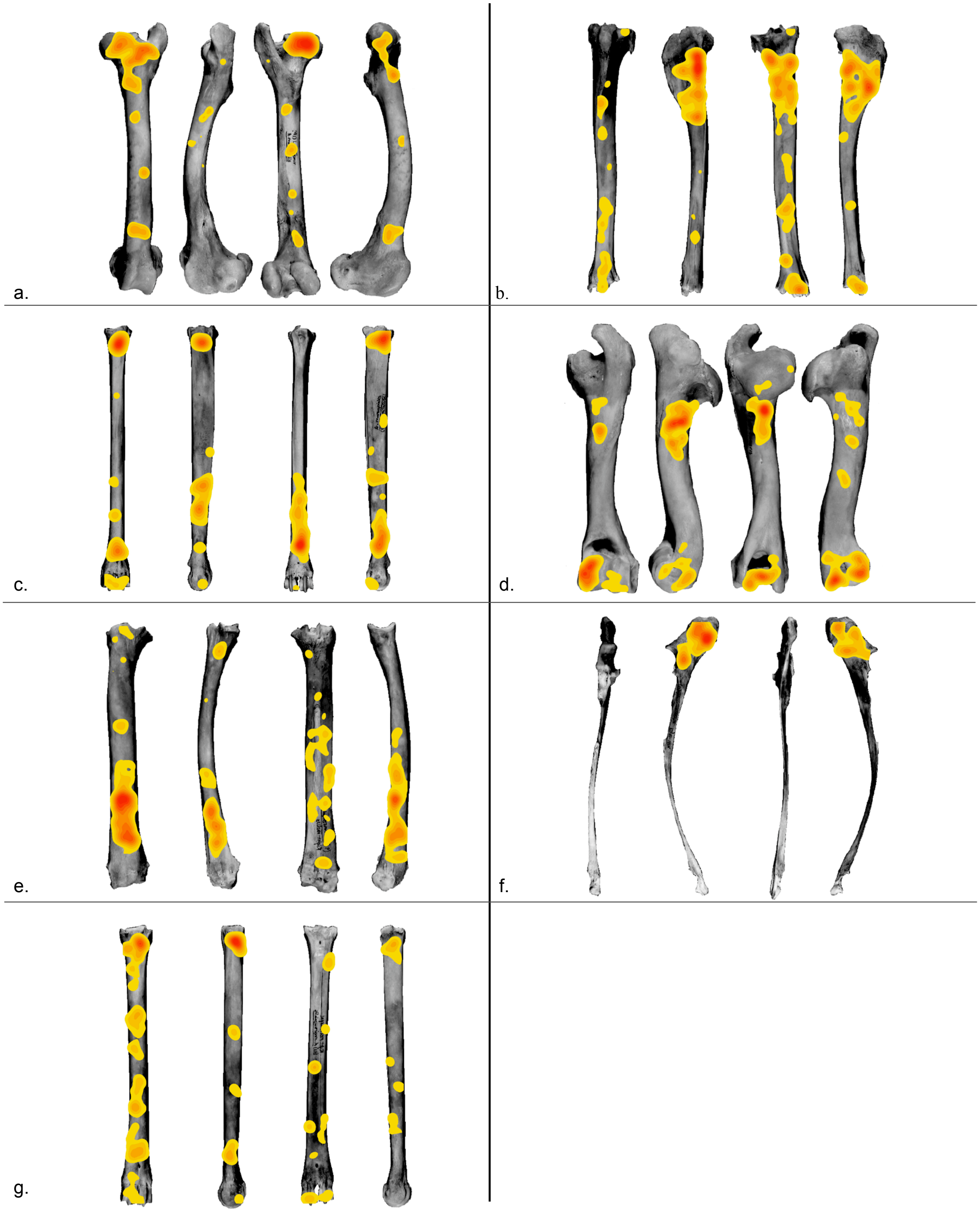


Table 1.1. GIS cluster analysis for tooth pits inflicted by wolf groups
Analysis was performed on four aspects of all left elements. The distance between each tooth pit and its nearest neighbor was measured. The nearest neighbor index (NNI) is the observed distance divided by the average expected distance in a hypothetical random distribution. If the NNI is less than 1, the pattern is considered clustered. If the NNI is greater than 1, the trend is toward dispersion. Asterisks appear next to p-values indicating significant clustering of tooth pits.

Element	**Small Group**				**Large Group**			
	Anterior	**Lateral**	**Posterior**	**Medial**	**Anterior**	**Lateral**	**Posterior**	**Medial**
Humerus	Random	Clustered	Random	Clustered	Clustered	Clustered	Clustered	Clustered
NNI	0.86	0.84	0.90	0.81	0.64	0.54	0.70	0.59
p	0.101	0.062	0.253	***0.001**	***<0.001**	***<0.001**	***<0.001**	***<0.001**
Radius	Clustered	Random	Clustered	Random	Clustered	Clustered	Clustered	Random
NNI	0.67	0.94	0.72	0.98	0.79	0.78	0.77	0.99
p	***<0.001**	0.618	***<0.001**	0.879	***<0.001**	***0.001**	***<0.001**	0.824
Ulna	N/A	Clustered	N/A	Clustered	N/A	Clustered	N/A	Clustered
NNI		0.64		0.47		0.73		0.53
p		***<0.001**		***<0.001**		***0.002**		***<0.001**
Metacarpal	Clustered	Clustered	Random	Clustered	Clustered	Clustered	Random	Random
NNI	0.67	0.67	1.01	0.72	0.82	0.58	1.06	0.94
p	***<0.001**	***0.001**	0.905	***0.005**	***0.001**	***<0.001**	0.513	0.551
Femur	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered
NNI	0.80	0.82	0.64	0.83	0.68	0.73	0.55	0.67
p	***0.004**	0.053	***<0.001**	0.080	***<0.001**	***0.002**	***<0.001**	***<0.001**
Tibia	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered
NNI	0.73	0.78	0.82	0.75	0.64	0.73	0.83	0.83
p	***0.002**	***0.001**	***0.001**	***<0.001**	***<0.001**	***<0.001**	***<0.001**	***<0.001**
Metatarsal	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered	Clustered
NNI	0.73	0.68	0.79	0.80	0.60	0.82	0.82	0.75
p	***0.003**	***<0.001**	***0.016**	***0.005**	***<0.001**	***0.002**	***0.006**	***<0.001**

Tooth mark frequencies

In order to facilitate comparison with other studies, I also present tooth mark frequency results as they have been traditionally quantified. Table 1.2 shows the percentage of tooth marked specimens for different long bone elements, broken down by bone region following Marean and Spencer (1991). More than 89% of the total number of identifiable size class 2

Table 1.2. Tooth mark frequencies for different wolf groups by bone portion

a. Tooth mark frequencies for large wolf group on size class 2 carcasses

Portion	Element													
	Femur		Tibia		MT		Humerus		Radius		Ulna		MC	
	TM	%	TM	%	TM	%	TM	%	TM	%	TM	%	TM	%
Proximal end	54/76	71.1	29/57	50.9	27/75	36	33/54	61.1	16/115	13.9	55/69	79.7	13/61	21.3
Proximal shaft	36/112	32.1	96/129	74.4	31/78	39.7	76/110	69.1	28/123	22.8	7/68	10.3	38/61	62.3
Middle shaft	28/114	24.6	49/139	35.3	27/76	35.5	32/120	26.7	62/122	50.8	3/61	4.9	21/61	34.4
Distal shaft	60/99	60.6	45/124	36.3	58/67	86.6	29/121	24	95/113	84.1	1/34	2.9	36/52	69.2
Distal end	24/52	46.2	28/92	30.4	5/6	83.3	70/115	60.9	5/15	33.3	0/5	0	8/35	22.9
Total	110/128	85.9	134/153	87.6	73/78	93.6	119/129	92.2	113/125	90.4	59/69	85.5	58/61	95.1

b. Tooth mark frequencies for Mexican Gray wolf pairs on size class 2 carcasses

Portion	Element													
	Femur		Tibia		MT		Humerus		Radius		Ulna		MC	
	TM	%	TM	%	TM	%	TM	%	TM	%	TM	%	TM	%
Proximal end	20/50	40	15/43	34.9	14/54	25.9	25/47	53.2	4/64	6.3	22/26	84.6	7/34	20.6
Proximal shaft	13/63	20.6	32/62	51.6	16/54	29.6	25/64	39.1	10/65	15.4	0/26	0	16/35	45.7
Middle shaft	9/64	14.1	11/63	17.5	18/53	34	5/68	7.4	17/64	26.6	1/26	3.8	10/34	29.4
Distal shaft	20/61	32.8	16/57	28.1	32/48	66.7	21/45	46.7	22/52	42.3	0/25	0	15/28	53.6
Distal end	24/55	43.6	6/41	14.6	9/20	45	32/66	48.5	10/16	62.5	0/10	0	16/21	76.2
Total	52/71	73.2	48/75	64	45/56	80.4	62/69	89.9	38/65	58.5	22/26	84.6	25/36	69.4

Table 1.2 continued

c. Tooth mark frequencies for red wolf pairs on size class 2 carcasses

Portion	Element													
	Femur		Tibia		MT		Humerus		Radius		Ulna		MC	
	TM	%	TM	%	TM	%	TM	%	TM	%	TM	%	TM	%
Proximal end	2/6	33.3	2/3	66.7	1/6	16.7	6/14	42.9	0/8	0	3/9	33.3	1/7	14.3
Proximal shaft	0/6	0	1/3	33.3	1/6	16.7	1/14	7.1	0/9	0	0/7	0	1/7	14.3
Middle shaft	0/7	0	0/3	0	0/6	0	0/14	0	4/9	44.4	0/7	0	2/6	33.3
Distal shaft	0/6	0	0/3	0	0/6	0	1/14	7.1	2/9	22.2	0/6	0	1/5	20
Distal end	1/7	14.3	1/2	50	1/5	20	3/11	27.3	1/4	25	0/5	0	0/5	0
Total	6/8	75	2/3	66.7	2/6	33.3	8/14	57.1	4/9	44.4	3/9	33.3	4/7	57.1

TM = number of tooth marked specimens (including tooth pits and scores) / total number of specimens in collection

Table 1.3. Percentage of total specimens in collection and percentage of midshaft specimens bearing tooth marks in wolf experiments

	NISP	NISP TM	% TM	Midshaft NISP	Midshaft TM NISP	Midshaft % TM
Size 2 Carcasses						
Large group	743	666	89.6	693	222	32
Small gray wolf group	398	292	73.4	372	71	19.1
Small red wolf group	56	29	51.8	52	6	11.5
Size 3 carcasses						
Large group	22	17	77.3	22	5	22.7
Small gray wolf group	5	5	100	5	2	40
Small red wolf group	3	3	100	3	1	33.3

NISP = number of identifiable specimens

specimens were tooth marked by the large wolf group (Table 1.3). Frequencies of damage by the wolf pairs in this study were somewhat lower at 73% for Gray Wolf pairs, and somewhat lower for the Red Wolf pairs at 52%.

The frequencies I report contrast with those reported by Stiner (2004) in the wolf-ravaged Late Pleistocene archaeological assemblages from Grotta di Sant'Agostino, Italy which show between 17 and 19% tooth mark damage in the total assemblage. The lower damage frequency seen in this archaeological context, however, may be due to temporal overlap and competition with hyenas and humans at the site, which may have decreased the wolves' access to carcass parts. My tooth mark frequencies are more in line with the frequency of 81% reported from feeding experiments by Castel (2004, Table 3) for sheep bones fed on by captive wolves. Haynes (1982) reports a tooth mark frequency of 75% for larger-sized, isolated *Bos* and *Equus* limb bones fed on by captive wolves. I did conduct feeding experiments with a smaller sample of size class 3 bison limbs, and found a tooth mark frequency of 77% produced by the large wolf group.

In terms of the distribution of tooth marks across bone elements, my results show that although all long bones were heavily tooth marked, there is a great deal of variation in the distribution of marks across different long bone portions. This finding is in agreement with reports by Faith (2007) and Kuhn et al. (2009), which also showed variability in tooth pit damage frequencies across bone portions for modern spotted hyenas (*Crocuta crocuta*). Particularly, I found an abundance of tooth marking on the proximal femur, proximal tibial shaft, distal radial shaft, and distal metatarsal. Metacarpals and metatarsals do not display the same pattern. I found comparably lower degrees of tooth marking on all long bone midshafts, except for the radius. The high degree of tooth marking seen on the metapodials was unexpected, given the relative lack of flesh on this element as well as the lower proportion of cancellous bone in the epiphyses.

Faith (2007) and Kuhn et al. (2009) have found that element portions with low bone density in most cases show a reverse correlation with tooth pit frequency in spotted hyena modified bone assemblages, whereby bone portions with low density are tooth marked at higher frequencies. This might be expected given that these low density, grease-rich areas are likely of most interest to carnivores. I have done a similar test on my canid modified assemblage to examine the relationship between tooth mark frequency (from Table 2a: large group) and bone density using density data reported for wildebeest by Lam et al. (1999) (Fig. 1.9). Results from my assemblage show a similar negative but non-significant relationship for proximal and distal epiphyses ($r = -0.324$, $p = 0.280$) and for proximal and distal shafts ($r = -0.324$, $p = 0.280$). In contrast to Faith's (2007) findings of a slight positive relationship between tooth mark percentage and bone density for hyena modified midshafts, I found a moderate, but non-significant negative relationship. The stronger, significant negative correlation Faith found for hyenas in the epiphyses and shaft ends might be expected given that hyenas tend to tooth mark at higher frequencies.

In comparison with tooth mark frequencies reported for other carnivore taxa (Fig. 1.10), my canid sample shows on average less damage than lions (Pobiner 2007). Given the range of variation in tooth mark frequencies reported for spotted hyena assemblages (Faith 2007; Kuhn et al. 2009), it is difficult to distinguish my canid sample from hyena modified samples.

Gross bone Damage Patterns

Delaney-Rivera et al. (2009) and Pobiner (2007) suggest that tooth mark frequencies paired with gross bone destruction patterns may provide the best resolution in identifying specific carnivore taxa responsible for modifying fossil assemblages. I report patterns of gross bone damage here to be considered in conjunction with the GIS analysis.

The few studies of large canid taphonomic signatures to date have mainly focused on patterns of gross bone damage. Haynes (1982, 1983) reported modifications to large bovid

Fig 1.9. Correlation between % tooth marked and bone density of wildebeest (Lam et al. 1999). (a) long bone proximal and distal epiphyses (*r* = -0.324, *p* = 0.280), (b) long bone proximal and distal shafts (*r* = -0.324, *p* = 0.280), (c) long bone mid-shafts (*r* = -0.665, *p* = 0.150).

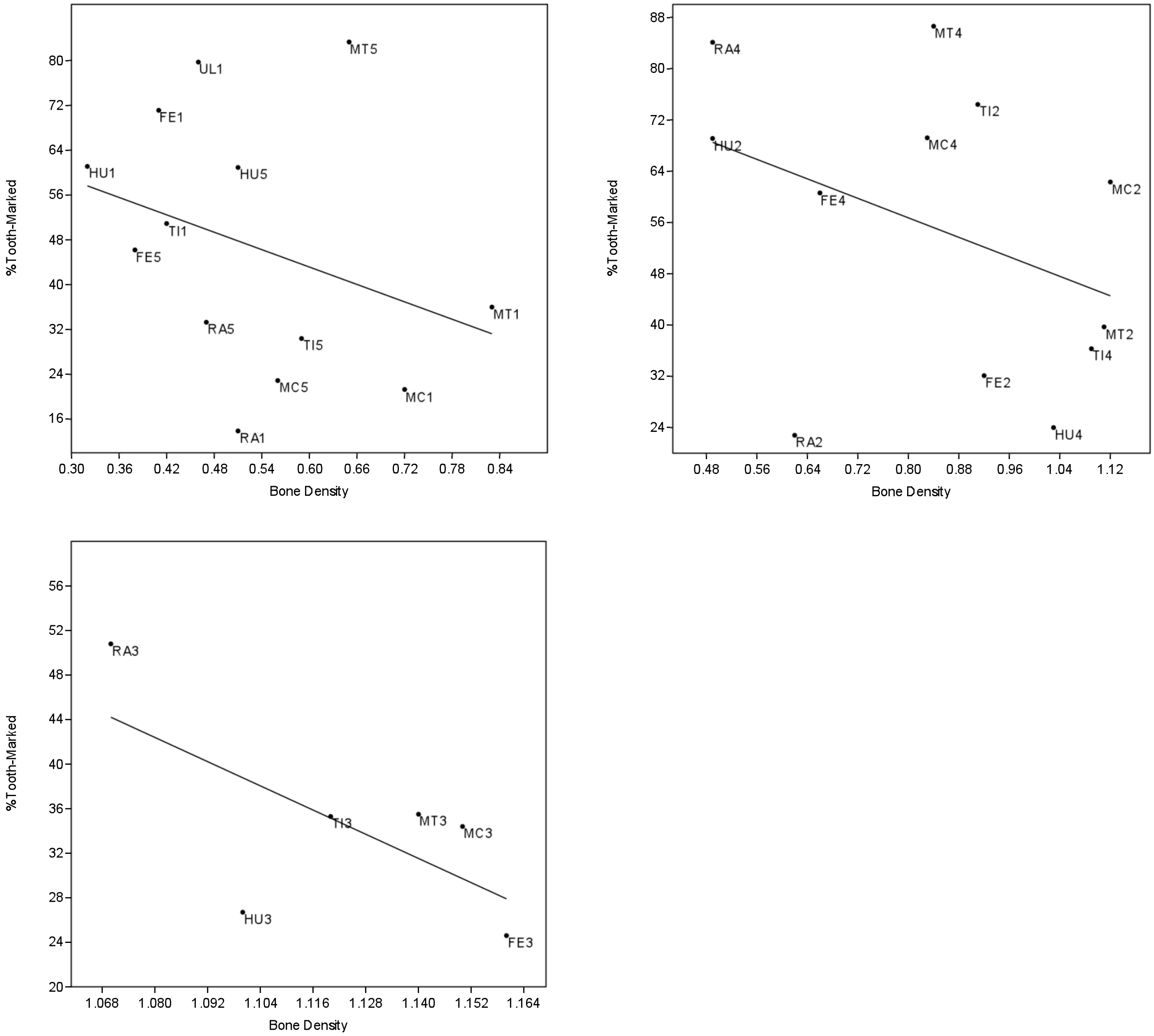
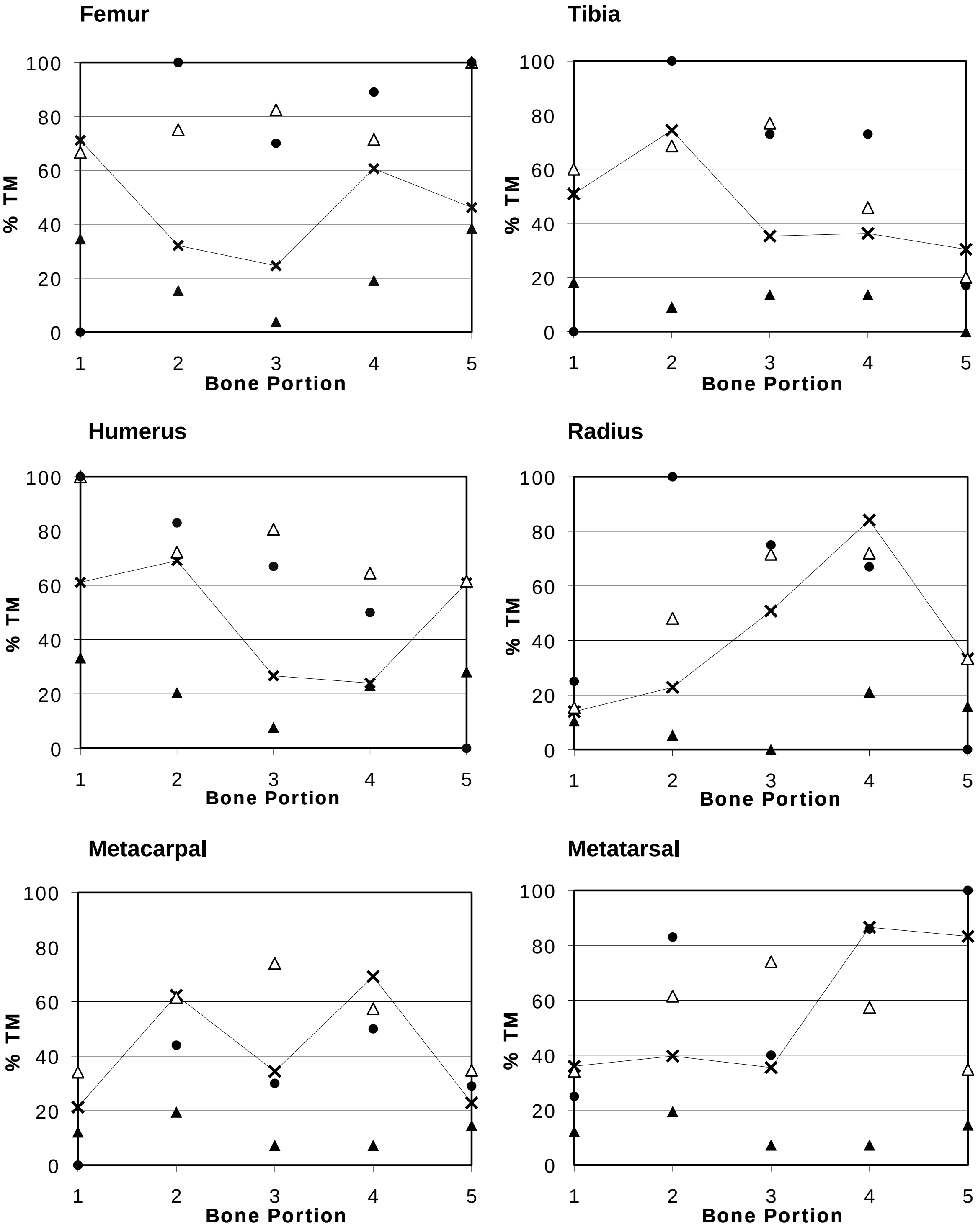


Figure 1.10. Tooth mark frequencies by element and portion for Gray wolf large group (this study) shown for comparison with datasets from other carnivore species. Hyena datasets present combined metapodial frequency counts, which I show separately for wolves.

—×— : Gray wolf large group
▲ : Spotted hyena (data from Kuhn et al. 2009, Table 4)
△ : Spotted hyena (data from Faith 2007, Table 4)
● : Lion (data from Pobiner 2007, Table 4.6)



Femur

Tibia

Humerus

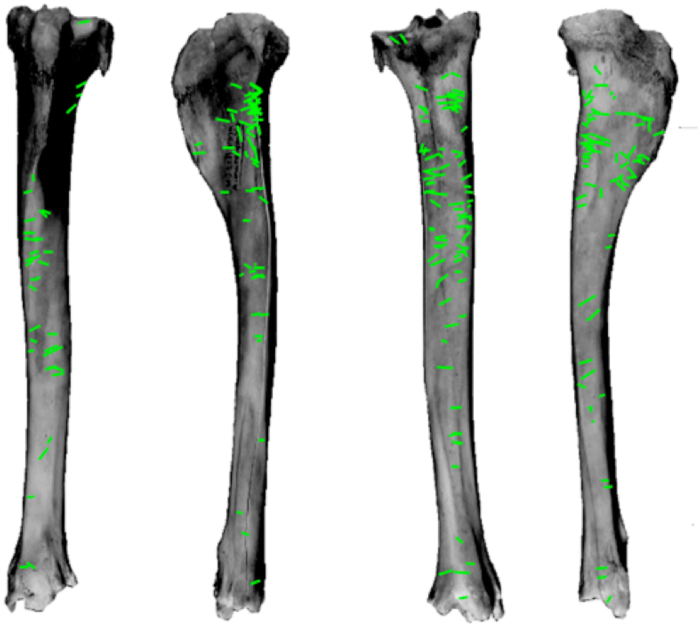
Radius

Metacarpal

Metatarsal

bones fed on by both wild and captive wolves (*Canis lupus*). The patterns I observed in gross bone damage in my assemblage of smaller carcasses are largely in agreement with observations by Haynes. In the most heavily utilized stage, long bones remain either as hollow cylinders, or as cylinders with one end missing. Tooth scores are most common near the ends and occur at right angles or diagonal to the long axis of the bone (Fig. 1.11).

Figure 1.11. **Composite GIS plot for tooth scores on the tibia illustrates tooth score orientation is typically at right angles or diagonal to the long axis of the bone.**



In their study of captive wolves, Campmas and Beuval (2008) concluded that the damage pattern wolves produced cannot be distinguished from the pattern produced by wild hyenas. They argue that the more intense damage inflicted on bones gnawed on by captive wolves versus their wild counterparts is likely the result of non-nutritional (recreational) gnawing. This difference, however, was seen only on bones of larger-sized prey animals. This underscores the importance of using either wild animals or captive animals fed a controlled diet which simulates circumstances in the wild in order to reduce the likelihood of recreational gnawing.

Table 1.4 summarizes patterns of gross bone damage seen in my experimental assemblage. The sequence of damage follows roughly the same pattern Haynes (1982) has documented for larger size class prey animals fed on by wild wolf packs, but the smaller (size 2) carcasses in my study were damaged more thoroughly in earlier stages of utilization. Figures 1.12-1.13 show some examples of specific types of damage seen in my experiments.

SUMMARY AND CONCLUSIONS

My results show that there is a great deal of variation in tooth mark frequencies among different long bone elements as well as among different element portions. This finding is in agreement with recent reports by Faith (2007) and Kuhn et al. (2009), which showed similar variability in tooth pit frequency across bones for modern spotted hyenas. Despite variation in tooth mark frequencies across bones, the GIS cluster analysis of experimental canid-gnawed carcasses was able to identify areas where significant clusters of tooth pits occur on all meaty limb bones. This underscores the contribution that the use of the GIS method brings to taphonomic studies.

Comparisons of tooth mark frequencies have been the main focus of studies attempting to interpret timing of access to carcasses by carnivores as well as carcass tissue yield across prehistoric faunas. I agree with Domínguez-Rodrigo (1997, 2002) that there should be increased specificity in documenting tooth mark placement. Because of the variation in patterns I identified across bone elements, I believe this study demonstrates the importance of separating analyses by element as well as bone portion. The GIS image analysis method is particularly well-suited to examine fine-level variation in tooth marking patterns and may have the potential to differentiate patterns produced by different carnivore taxa.

Table 1.4. Patterns of gross bone damage in bones gnawed on by wolves.

	Light - moderate utilization	Heavy utilization
Femur	- Cheek teeth penetrate epiphyses. - Greater trochanter and distal epiphysis completely removed. - Tooth marks gouge and undercut femoral head, but head usually remains intact.	- Distal end gone. Proximal end may be gone or nearly gone. - Heavy tooth pitting on proximal end. - Tooth scores on distal shaft transverse to long axis of bone. - Fracturing of shaft.
Tibia	- Proximal epiphysis completely removed and consumed. - Crest removed. - Large sections of the shaft may be levered off from the lateral aspect.	- Proximal half usually absent. - Distal epiphysis may be attached to a section of midshaft. - Distal end may show intensive tooth pitting.
Humerus	- Greater tuberosity is gnawed and may show furrowing – in more moderate utilization it is completely removed. - A portion of the head may remain, but is heavily tooth marked.	- Proximal epiphysis completely consumed. - Gnawing proceeds from proximal end with flakes of midshaft levered off. - In final stages, only distal end remains, with medial and lateral condyles removed and furrowed.
Radius	- May be complete with tooth pitting present on distal epiphysis or distal epiphysis may be removed with intensive tooth pitting and scoring on broken distal end. - Gnawed distal end may show rounded edges.	- Distal end is gone. - Sections of midshaft are levered off. - Proximal end remains intact, with minimal tooth marking.
Ulna	- Tooth pitting present on superior aspect of olecranon process. - Distal end may be snapped off.	- Olecranon process is progressively consumed down to the semilunar notch. - intensive tooth pitting and scoring visible on remaining stump of olecranon. - Distal half is usually gone.
Metapodials	- Bone is typically intact with tooth pitting on distal epiphysis.	- Distal epiphysis chewed off and shaft progressively consumed from distal end. - Gnawed edge of distal end shows intensive tooth marking and rounded edges. - Proximal end is almost always present.

Figure 1.12. Examples of canid damage to size 1 and 2 hind limb bones in this study.
a. Range of damage seen on the femora, posterior view, b. Typical damage to proximal femur, anterior view (left) and posterior view (right), c. Typical damage to metatarsal, anterior view, d. Range of damage seen on tibiae, anterior view, d. Typical damage to the proximal tibia, anterior tuberosity gnawed away.

Figure 1.13. Examples of canid damage to size 1 and 2 fore limb bones in this study.
a. Range of damage seen on the humerus, posterior view, b. Typical damage to humerus. Note damage to epicondyle, c. Range of damage seen on the radius, anterior view, d. Range of damage seen on the ulna.

Utility of the GIS Image analysis Method

The potential of the GIS spatial statistical tools described in this study to quantify and analyze bone surface modification patterning provides an improvement on existing methods which also map bone surface modifications onto template graphics (e.g., Domínguez-Rodrigo and Barba 2006, Domínguez-Rodrigo et al. 2007a) by allowing for more powerful statistical analyses. Rather than classifying modifications into one of several pre-defined zones as other methods have done (e.g., Domínguez-Rodrigo 1999; Marean and Spencer 1991), GIS cluster analysis identifies important zones based on statistically significant clusters of modifications. Each individual modification can be linked back to a complete database that contains specific information about the modification as well as information about the fragment on which it occurs. This method of data storage becomes extremely convenient in a large assemblage. The database can be queried by any variable included within it (e.g., taxon, size, provenience). Furthermore, because bone surface modifications are spatially linked to fragment files, these modifications can be examined relative to bone portion survival. The spatial linkage of information and powerful analytical tools provided within ArcGIS allow for numerous and flexible possibilities in the way data can examined. Using GIS to document bone fragment data can be more time consuming than other approaches, but in my experience it is worth this effort for the greater spatial precision in data recording and greater flexibility in the way research questions can be addressed.

There is great potential for using the GIS image analysis method to build models for the interpretation of zooarchaeological assemblages. Analyses of modern experimental bone assemblages using this GIS method can provide valuable analogs with which to compare tooth mark and butchery mark distributions in fossil assemblages. While the assemblages in this study model only large canid access, in the future I plan to analyze data from assemblages modified by other large carnivores, as well as humans, in different orders of access. The relationship between butchery mark and tooth mark clusters in an archaeofaunal assemblage could indicate where differences exist in the type of tissue being extracted, and allow for an assessment of variation in carcass use between hominins and carnivores. This study serves as a demonstration of some of the analytical possibilities available with this software. It is my hope that the methodology employed here will encourage greater standardization in zooarchaeological data recording.

SUPPLEMENTARY MATERIAL TO CHAPTER 1: ArcGIS METHODS

A detailed description the GIS image analysis system has been provided in the "Bone Entry GIS and Bone Sorter Manual," which is available along with the Bone Entry GIS program as supplementary material to Marean et al.'s (2001) paper. As steps for MNE analysis are outlined in detail in this manual, they will not be reiterated here. I will outline only the deviations I have taken from and additions I have made to the method as originally described.

Data entry was conducted using Marean's (2001) method as originally described. The density and nearest neighbor distance functions outlined below are new additions I have made based on some of the functions available in newer versions of ArcGIS.

Bone Portion Survivorship

I used the ArcView platform for data entry, as the scripts available in Bone Entry GIS automate portions of the fragment entry and initial grid conversion. Data entry can also be accomplished without use of the scripts in more recent versions of ArcGIS by creating new layer files individually.

In order to build models for bone portion survivorship, I followed the steps outlined for bone fragment entry and MNE analysis in Marean et al.'s guide. I used Marean's MNE steps 1-3 to create MNE "maps." These steps are summarized as follows:

> Step 1 joins an external database to the attribute tables of each fragment (layer) file. The database can then be queried to select fragment files to be included in the MNE map.
>
> Step 2 converts the selected layers which were drawn as vector images to grid files.

Step 3 adds the grid files together into a composite grid representing bone portion survivorship in a the element under analysis.

Density Analysis – Kernel Density

I used a kernel density calculation to graphically display tooth mark cluster distribution across bone elements. This tool takes a point feature (e.g., tooth pit layer) and builds a rasterized image of point clustering. This tool uses the quadratic kernel formula described in Silverman (1986, p. 76) to fit a smoothly tapered surface to each point, which spreads out to a specified radius around the point. The highest cell value (1) is at the point location in the center of the spread, with the value tapering to zero at the boundary of the search radius distance. The sum of the intersecting spreads is then calculated for each cell in the output raster (ESRI 2011). Using this kernel function rather than the simple point density function effectively takes into account the margin of error that may be associated with hand-plotting the tooth mark location points on the original GIS template, by weighting cell values in a radius surrounding the point.

Figure 1.14. Illustration of Kernel Density analysis

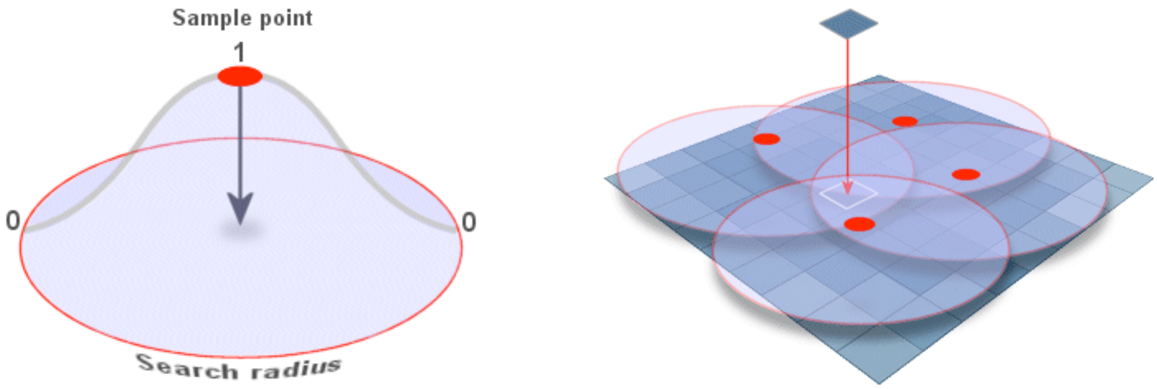


Image courtesy of Jochen Albrecht

Kernel density images were generated using the following parameters:

Arc Toolbox → Spatial Analyst Tools → Kernel Density

In the Kernel Density dialog box:

- Input point or polyline features = the point layer to input for density analysis
- Population field = NONE (Inserting a numerical value here will determine how many times the point will be counted.)
- Output raster = name the output raster here
- Output cell size = I use a cell size of 5, which is reduced from the default size. Decreasing the cell size generates a raster with finer resolution and smoother contour lines.
- Search radius = I used a standard search radius of 225 cells for each analysis.

To eliminate single point outliers in the output raster, I manually increased the boundary of the lowest classification break (no data). This is done by opening “layer properties” and selecting Symbology → Classification → Classify. The break value for the lowest value was increased until single points were no longer shaded in the raster display.

Average Nearest Neighbor Distance

The Average Nearest Neighbor Distance tool was used to measure the distance between individual tooth marks and to test for significant spatial clusters. If the average distance between points (tooth marks) is less than the average for a hypothetical random distribution, the distribution is considered clustered. The NND is expressed as a ratio of the observed distance divided by the expected distance. If the index is less than 1, the pattern is considered clustered. If it is greater than one, the pattern is considered dispersed.

This tool is accessed in ArcToolbox through:

Spatial Statistics tools → Analyzing Patterns → Average Nearest Neighbor

Before computing the NND, the study area should be determined. The default study area for the NND calculation is the minimum enclosing triangle that would encompass all features (pits) in the selection. Because bones are not triangles, the study area needs to be corrected to represent the size of the bone template accurately. This can be done using the Calculate Area tool as follows:

- In ArcToolbox, select: Utilities → Calculate Areas
- Input feature class = select the bone template shape file to calculate areas for
- Output feature class = this will output a shapefile with a column in its attribute table that has the area of each polygon feature (F_AREA)

The average nearest neighbor distance is calculated for each element and each view (anterior, lateral, etc.) as follows. The NND should be calculated for each view separately in order to accurately represent the surface area of the bone.

- In the tooth pit layer, highlight (select) all pits in a single view (e.g., all tooth pits on the anterior aspect of the femur).
- In ArcToolbox, select: Spatial Statistics tools → Analyzing Patterns → Average Nearest Neighbor
- Input Feature Class = the name of the tooth pit layer file in which the pits are selected
- Distance Method = Euclidean distance
- Area = the area for that bone template polygon, which is derived from "Calculate Area" above
- The analysis will output the NND ratio, Z score, and *p*-value.

Chapter 2. Characterizing Felid Tooth Marking and Gross Bone Damage Patterns Using GIS Image Analysis

ABSTRACT

In recent years there has been much disagreement over the nature of carnivore involvement in Early Pleistocene zooarchaeological assemblages. This partially reflects the lack of reliable ways to identify the taphonomic signatures of different large carnivore taxa. It is often unclear which carnivore taxon or taxa may have played a role in forming or modifying faunal assemblages found associated with stone tools, and this lack of clarity impacts reconstructions of hominin behavior. The mode, frequency and nutritional yield of carcasses acquired by hominins, and the extent to which hominin foraging impinged on or was constrained by the guild of large predators is a topic of great importance.

This paper characterizes the taphonomic signature of large felids using a GIS image analysis method to study tooth marking and gross bone damage on neotaphonomic experiments carried out with tigers (*Panthera tigris*) and African lions (*Panthera leo*) at the Carolina Tiger Rescue (Pittsboro, North Carolina). This is the largest experimental assemblage demonstrating the impact of felid feeding on bone preservation to date. A typical pattern of bone damage resulting from large felid carcass modification is identified, and this pattern can be distinguished from bone damage patterns produced by hyaenids. In summary, this pattern consists of tooth marking largely restricted to limb bone ends and minimal bone fragmentation.

INTRODUCTION

The ability to better distinguish between the taphonomic signatures of large carnivores from the East African Plio-Pleistocene will provide better resolution to questions about the scale and frequency of hominin access to large mammal carcasses. These questions include whether hominins were scavenging from felid kills, with or without subsequent hyaenid consumption of the debris left by hominins (Blumenschine 1987, 1995; Selvaggio 1998; Pante et al. 2012), or whether hominins had early access to carcasses, potentially through hunting (Bunn and Kroll 1986; Potts 1988; Oliver 1994; Domínguez-Rodrigo 2002, 2009; Plummer 2004; Domínguez-Rodrigo et al. 2007a; Ferraro et al. 2013). Although this has been a debate in the literature for some time (Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003, Domínguez-

Rodrigo and Barba 2006; Blumenschine et al. 2007) there has been no systematic study that has described and been able to differentiate the gnawing patterns produced by hyenas and large felids. As interpretation of the context of hominin and carnivore activities at some early zooarchaeological sites hinges on identification of the particular carnivore taxa involved, characterizing the patterns produced by different large carnivores is of great interest to zooarchaeologists.

The potential for felid involvement in Early Stone Age (ESA) site formation has played a pivotal role in some arguments for hominin carcass access at Oldowan sites (see Chapter 4 for a detailed discussion). Domínguez-Rodrigo (2007b, 2009) has criticized some studies for using hyena tooth mark frequencies from experimental contexts (Blumenschine 1995; Capaldo 1995) or tooth mark frequencies of various carnivore species tallied together (Selvaggio 1994) to generate models of carcass access where felids are purported to be the initial consumer. This criticism is theoretically valid, as felids are flesh specialists, and should be expected to modify bones differently than hyenas, which have adaptations for bone crushing. However, we have until recently lacked robust models for felid bone modification.

The Large Felid Dietary Adaptation: Hypercarnivory

The extant felids are unique among the carnivores in their dietary homogeneity. They are characterized as hypercarnivorous (flesh specialist) in their dietary behaviors (Holliday et al. 2001, 2004; Van Valkenburgh 2007; Hartstone-Rose 2011) as opposed to durophagous (bone crushing) (Werdelin and Solounias 1991). Some larger-sized felids (e.g., African lions and mountain lions, *Panthera leo* and *Felis concolor,* respectively) have been observed on occasion to consume small pieces of bone, often from juvenile individuals (Schaller 1972; Blumenschine 1987; Stiner et al. 2012). However, the bulk of the large felid diet is composed of flesh, which may include smaller amounts of skin and connective tissue, but very little actual bone. Cheetahs have not been observed to consume bone at all (Van Valkenburgh 1996). This dietary homogeneity is also reflected in felid dental morphology. Extant felids are recognized as one of the most morphologically uniform families among the carnivores (Hartstone-Rose 2008). Despite their lack of bone-cracking capabilities, large felids do tooth mark bones (Selvaggio 1994a,b; Cavallo and Blumenschine 1989; Pobiner 2007; Gidna et al. 2013). The question then remains: how can the large felid taphonomic signature be characterized and distinguished from that of other large carnivores, particularly from hyenas, whose bone damage pattern is better known?

Background: Previous Studies of Felid Bone Modification

Felid Tooth Mark Studies

Selvaggio (1994a,b) conducted some important early studies that compared observations of carnivore feeding behaviors and carcass abandonment in the Serengeti and Ngorongoro Crater to results of experimental butchery of long bones collected after carcasses were abandoned by carnivores (to simulate hominin scavenging). As her goal was to gauge the effect of carnivore group size on the potential for scavengable tissues after carcass abandonment, she did not report her data separated by carnivore taxon, but by number of carnivores in the group. Bones in her sample were observed being modified by lions, leopards, cheetahs, spotted hyenas and jackals. Selvaggio reports tooth mark frequencies on complete bones from her assemblage to be approximately 50% (1994a, Table 2). This frequency is lower than those that have been reported for hyena-modified assemblages, which are typically greater than 75% (e.g., Blumenschine 1995). Domínguez-Rodrigo (2009) has argued that because Selvaggio’s experiments mix high tooth-marking and low-tooth marking carnivore taxa, they obscure contributions made by different predators, and cannot be used as reliable models. Selvaggio's experiments also mix together different prey sizes. Although Selvaggio's work is an important early contribution to modeling carnivore damage to bones, current neotaphonomic work must control for prey size and carnivore taxon in order to build the most robust experimental models.

In addition to reporting the overall frequency that bones were tooth marked in her study assemblages, Selvaggio examined tooth mark density (number of marks per bone) in her felid-derived assemblages. She found that 75% of the specimens have tooth mark densities <21 marks per bone. Tooth mark densities reported for assemblages modified by hyenas have usually been reported to be >70 marks per bone (Selvaggio 1994b). Selvaggio's results indicate that the density as well as the frequency of tooth marks left by felids on limb bones is much lower than that of hyenas.

Flesh Availability on Felid Kills and Modeling Scavenging Opportunities for Plio-Pleistocene Hominins

An important focus of some studies of felid feeding behavior has been the documentation of flesh availability following felid carcass abandonment (Blumenschine 1987, 1988; Cavallo and Blumenschine 1989; Selvaggio 1994a; Domínguez-Rodrigo 1999; Pobiner 2007). These studies have been carried out to assess potential scavenging opportunities for hominins in their transition from a plant-based diet to a diet that included greater amounts of animal tissue.

Blumenschine (1987) conducted one of the first experimental studies of carnivore carcass processing behaviors, in which he proposed a scavenging niche for early hominins. This study examined modern scavenging opportunities in the Serengeti and Ngorongoro Crater in Tanzania in an attempt to model scavenging opportunities that may have been available to early hominins. He examined 264 large herbivore carcasses in a variety of habitat settings and measured carcass quality for scavenging by the amount of edible tissue remaining after consumption by the initial predator, as well as the length of time the carcass persisted as a scavengable food source. He found that the initial consumer has a major impact on carcass persistence. Hyenas, with their jaw specializations for bone crushing, often fully consumed carcasses, while lions, which do not have this adaptation, are restricted to flesh and viscera. Blumenschine also found that carcass availability varied according to ecological context (e.g., season, habitat type, and degree of competition). Rainfall seasonality leads to seasonal fluctuations in plant growth, which in turn lead to herbivore migrations. The concentration of herbivores will affect the degree of competition in a given environment. Blumenschine noted that in the Serengeti, there is high competition during the wet season when herds are absent. However, during the dry season, herds migrate to more wooded areas where there are water sources and competition levels are reduced. He also noted that lions prefer to hunt in these wooded habitats, so carcass persistence is generally longer, due to the absence of hyenas which prefer more open habitats. Blumenschine argued that if these modern ecological parameters also characterized prehistoric ecosystems, early hominins may have found a dry season scavenging niche in wooded areas. The even greater diversity of felids in the Plio-Pleistocene may have provided abundant carcasses from which hominids may have scavenged within-bone tissues, particularly in woodlands.

Blumenschine and colleagues subsequently used their actualistic work to build an argument for a three stage (carnivore-hominin-carnivore) model of carcass access to explain bone damage patterns seen at the 1.84 Ma archaeofaunal assemblage from FLK 22 (FLK Zinj) at Olduvai Gorge, Tanzania (Blumenschine 1995; Capaldo 1997, 1998; Selvaggio 1998). According to this model, hominins scavenged the largely defleshed, but marrow-filled limbs abandoned by felids. Following hominin demarrowing of limb bones and scavenging of brains, hyenas (which have bone-cracking adaptations) scavenged the grease-rich epiphyses that remained on site.

Domínguez-Rodrigo has since argued against the three stage model of carcass access at FLK Zinj (Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo et al. 2007a) based on experiments which examined the anatomical distribution of flesh scraps on a sample of lion kills (Domínguez-Rodrigo 1999). He found that lions almost always completely deflesh carcasses, leaving few edible flesh remains. Of the flesh scraps that were preserved on lion kills in his study, over 80% were on intermediate (radius and tibia) limb bones. Flesh was rarely found on the meatier, upper limb bones. These findings led Domínguez-Rodrigo to suggest that scraps of flesh do not survive lion consumption as commonly as was originally thought (Domínguez-Rodrigo and Barba 2006). Selvaggio’s (1994b) observations showed a similar pattern where upper limb bones (femora and humeri) were normally abandoned by lions with little or no flesh remaining.

Pobiner (2007, 2008) has provided a valuable description of felid bone modification patterns based on carcasses fed on by several species of both wild and captive felids. Her study showed in some instances greater survival of flesh following lion consumption, and increased the range of variation known for lion feeding traces. Pobiner (2007) was also the first to fully report tooth mark frequencies that were clearly attributed to felids, as well as the first to quantify gross bone damage by felids. The study presented here builds on Pobiner’s work, using her radial diagram method for gross bone damage recording in addition to the GIS image analysis system to document patterns of large felid carcass modification in a larger sample of 46 experiments.

SAMPLE AND METHODS

Felid Feeding Experiments at Carolina Tiger Rescue

Feeding experiments were carried out with captive tigers and lions during 2010 at Carolina Tiger Rescue (CTR; formerly the Carnivore Preservation Trust), a non profit animal sanctuary in Pittsboro, North Carolina. The animals at this sanctuary are housed in large, natural habitat enclosures as individuals or pairs and are exclusively fed a natural, whole-carcass diet mainly consisting of chickens and deer. The experiments involved 15 tigers (*Panthera tigris*) and 3 African lions (*Panthera leo*) (Fig. 2.1). All individuals in this study were adult. In these experiments, whole deer carcasses or half carcasses were fed to felids at regular feeding intervals (Table 2.1). All carcasses fall within the bovid size class 1 or 2 category of Bunn (1982). Carcasses were obtained by CTR as road kill from the North Carolina Department of Transportation or through donations by local hunters. The road kill carcasses were gutted to ensure safety of the meat for carnivores. Carcasses were left in the felid enclosures for approximately 48 hours, after which the enclosures were completely cleaned of remaining carcass portions and all visible bone fragments. During collection of carcass remains, detailed notes were taken on the anatomical locations of surviving flesh. Bones and remaining carcass parts were frozen in bags separated by experiment until the time of cleaning.

The carcasses were largely intact when collected, and some flesh and tendon remained on the bones. Bones were degreased and cleaned of these remaining tissues by boiling in a mild solution of water and laundry detergent in the Anthropology Bone Research Laboratory at Queens College. All bones in the sample were examined with a 10x hand lens under oblique light to identify tooth marks. Tooth marks were identified based on published criteria (Binford, 1981; Bunn, 1981; Blumenschine et al. 1996; Domínguez-Rodrigo and Barba 2006).

Figure 2.1. Study animals at Carolina Tiger Rescue.
(a) Moki, (b) Background is Mona, foreground is Moki, (c) Rajaji, (d) One of the enclosures

(a)

(b)

Figure 2.1 continued

Table 2.1. List of Carolina Tiger Rescue experiments. All study animals are tigers unless otherwise noted. Study animal names marked with an asterisk are lions. All carcasses are deer unless otherwise noted. n.d. = no data.

Experiment	Study animal	Date fed	Date carcass removed	Carcass type
1	Rajah	10/3/2010	10/5/2010	1/2 Rear (Separated behind rib cage)
2	Keala	10/3/2010	10/5/2010	1/2 Front (Separated behind rib cage)
3	Tex	10/6/2010	10/8/2010	1/2 Front
4	Jelly Bean	10/6/2010	10/8/2010	1/2 Rear
5	Lucky	10/7/2010	10/9/2010	1/2 Rear, Back straps removed
6	Carmelita	10/7/2010	10/9/2010	1/2 Front, Back straps removed
7	Rajaji	10/7/2010	10/10/2010	1/2 Rear
8	Vincent	10/7/2010	10/9/2010	1/2 Front
9	Mona	10/9/2010	10/13/2010	1/2 Front
10	Moki	10/9/2010	10/13/2010	1/2 Rear
11	Nitro	10/9/2010	10/13/2010	1/2 Rear
12	Apache	10/9/2010	10/13/2010	1/2 Front
13	Rajah	10/10/2010	10/13/2010	Whole
14	Vincent	10/23/2010	10/25/2010	Torso (with neck attached – some fur left on neck, but no fur on body). No legs attached. No extra meat taken off.
15	Rajaji	10/27/2010	10/29/2010	Front cow leg (Most of meat removed)
16	Mona	10/30/2010	11/1/2010	Whole
17	Moki	10/30/2010	11/1/2010	Whole
18	Tex	11/1/2010	11/3/2010	Torso (with neck attached, no fur, backstraps removed)
19	Jelly Bean	11/1/2010	11/3/2010	Whole (backstraps and meat off back legs removed)
20	Apache	11/1/2010	11/3/2010	Whole (small deer)
21	Nitro	11/1/2010	11/3/2010	Torso (small deer, backstraps removed, no fur) + 4 deer legs separated (no fur, lower joint and down removed)
22	Moki	11/18/2010	11/21/2010	Whole
23	Vincent	11/20/2010	11/23/2010	1/2 Front
24	Keala	11/20/2010	11/23/2010	Whole
25	Carmelita	11/20/2010	11/23/2010	Whole
25b	Lucky/ Carmelita	11/20/2010		Whole
26	Jelly Bean	11/20/2010	11/23/2010	Whole (backstraps removed)
27	Nitro	11/20/2010	11/23/2010	Whole
28	Vincent	11/27/2010	11/30/2010	Ribs, left leg, spine (back strap removed), no pelt
29	Mona/Moki	11/29/2010	12/2/2010	Whole
30	Lucky/ Carmelita	11/29/2010	12/2/2010	Whole
31	Rajaji	12/4/2010	12/7/2010	Deer torso (neck, rib cage, spine – back straps removed)
32	Mona	10/3/2010	12/7/2010	Front 1/2 of deer with 2 legs
33	Moki	10/3/2010	12/7/2010	Back 1/2 of deer with 2 legs
34	Carmelita	10/6/2010	12/8/2010	Deer torso (neck, rib cage, spine – back straps removed) no pelt
35	Lucky	10/6/2010	12/8/2010	Deer torso (neck, rib cage, FL leg with fur, spine – back straps removed)
36	Rajaji	12/11/2010	12/16/2010	Deer neck, body, 1 FL leg, 2 back legs, spine, all meat still in tact, with pelt
37	Vincent	12/11/2010	12/17/10	Small whole deer (pelt, 4 legs)
38	Nitro	12/12/2010	12/17/10	Back 1/2 of deer with 2 legs and pelt

Table 2.1 continued

39	Apache	12/12/2010	12/17/10	1/2 of deer, split down middle (half of torso, one front leg, one back leg, pelt included)
40	Titan/Bali/ Java	1/5/2011	1/7/2011	Each fed 1 large calf leg each (2 front legs, 1 back leg)
41	Titan/Bali/ Java	1/7/2011	1/9/2011	Deer torso, 4 deer legs (only cleaned half of enclosure - were fed in the section cleaned)
42	Sebastian*, Sheba*, Tarzan*	1/19/2011	1/21/2011	Deer torso (neck, body, no legs), 2 back legs (already separated)
43	Rajaji	2/21/2011	2/23/2011	Rear 1/2
44	Vincent	2/21/2011	2/23/2011	No feeding notes – only rib fragments remained
45	Mona/Moki	1/21/2011	n.d.	n.d.
46	Sebastian*, Sheba*, Tarzan*	2/19/2011	n.d.	Pony hind limb - size 3

Gidna et al. (2013) have criticized the validity of using experimental models created from feeding experiments with captive animals. Removed from their natural environment, captive animals do not normally experience intra-group competition and thus have more time to spend with carcasses. This can contribute to higher degrees of gross bone damage. Captive animals are also documented to display a range of stereotypical behaviors due to the monotony experienced in their unnatural, enclosed environments, which may include boredom chewing of bones. A typical zoo diet of deboned flesh or other zoo-formulated foods can also cause carnivore teeth to wear abnormally, and thus may affect tooth marking patterns seen in experiments. Because of their naturalistic captive conditions, the animals at the Carolina Tiger Rescue are not subject to these criticisms. The animals at CTR are kept in grassy and wooded enclosures one acre or larger in size. They are routinely fed a whole-carcass diet several times a week, and are not overfed. The whole-carcass diet mimics the mechanical properties of wild felid foods, and thus tooth wear and masticatory musculature in these animals is analogous to that of wild felids (Hartstone-Rose et al. 2012). CTR animals are also given ample enrichment activities to stave off abnormal behaviors due to boredom.

My analysis is focused on the long bones from the felid feeding experiments because of their high representation in archaeological bone assemblages. These bone have a high survivorship potential (Faith and Gordon 2007), and thus are the least likely to be subject to other taphonomic agencies. I will also address some gross bone modification patterns observed in the scapula and pelvis. I consider both lion- and tiger-modified experiments together as their cranial and dental morphologies are virtually indistinguishable (A. Hartstone-Rose, pers. comm.), and I did not observe a difference in their bone modification patterns.

GIS Image Analysis Method

I use the GIS image-analysis approach originally described by Marean et al. (2001) and expanded on here in Chapter 1 to visualize patterns of bone portion survivorship, as well as to analyze the distribution of carnivore tooth marks in this assemblage. To examine bone portion survivorship, images of each fragment in the collection were digitally drawn over a photographic template of a complete element. These images were then overlapped to form a composite image illustrating which bone portions are frequently preserved, and which are frequently deleted by carnivore consumption. Tooth marks were also spatially plotted on bone templates in GIS to produce composite images of tooth mark distribution for each element. The Density and Analyzing Patterns toolsets within ArcGIS were then used to analyze tooth mark clustering patterns following the method fully described in Chapter 1 and supplementary material to Chapter 1.

RESULTS – GIS IMAGE-ANALYSIS

Bone Portion Survivorship

Figure 2.2 shows results of the GIS-generated maps of bone portion survivorship for long bones of size class 1 and 2 carcasses. Sample sizes for size class 3 were not large enough for GIS image analysis, but will be considered separately under “Gross Bone Damage” below. These images represent composites of both left and right elements in the assemblage. To create these composites, the right element fragments were drawn over a template of a complete right element in GIS. The right fragment images were then mirrored over the left to create right/left composites.

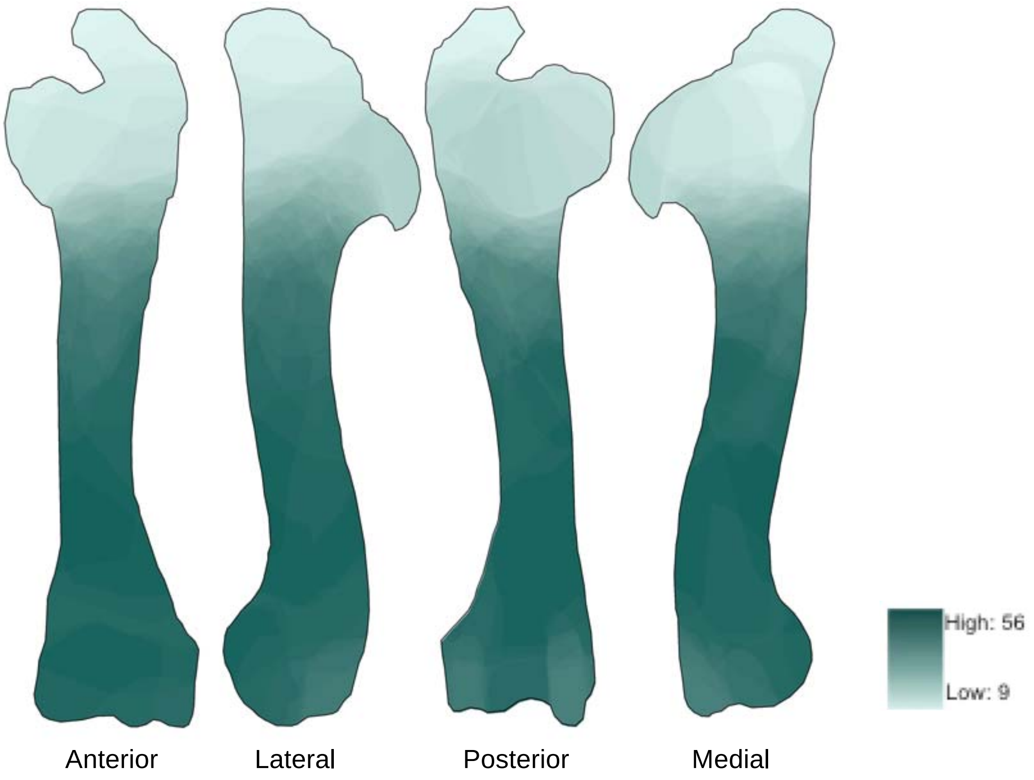
Forelimb

As illustrated in Figure 2.2, the humeral head is nearly always destroyed. In fact, only 9 specimens out of a total of 56 humeri preserve the humeral head. The distal humerus and humeral shaft are preserved at much higher rates. The radius is nearly always preserved complete. The distal radius is in some cases gnawed, but 45 specimens out of 56 in the collection still preserved the distal epiphysis intact. The olecranon process of the ulna is normally consumed. Metacarpals are usually complete, but when damaged, they are gnawed from the proximal end.

Hindlimb

Bone preservation in the hindlimb shows the compact bone of the femoral shaft is well preserved, but the proximal and distal epiphyses are sometimes destroyed. The greater trochanter is particularly prone to destruction. The proximal end of the tibia is not well preserved, but the shaft and distal end are normally intact. Finally, metatarsals are well preserved, but when damaged, gnawing occurs from the distal end, leaving the proximal end intact. This is opposite the pattern seen in the metacarpals where gnawing originates from the proximal end and moves downward.

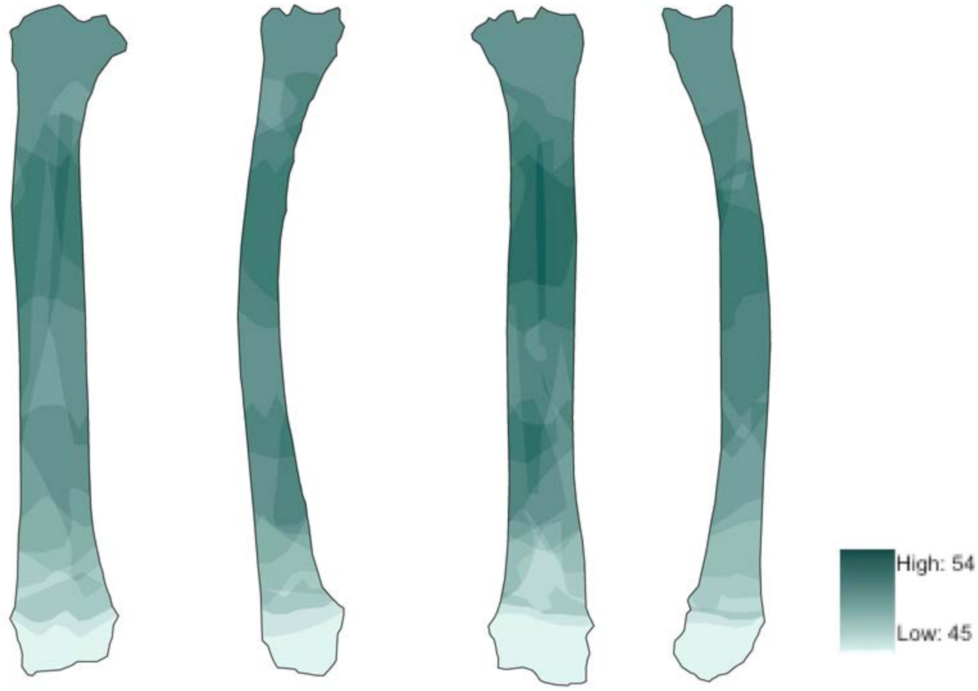
Figure 2.2. Bone preservation in Carolina Tiger Rescue experiments for size 1-2 carcasses. Dark shaded areas indicate areas of highest survivorship (highest number = MNE). Light areas indicate lowest survivorship. Colors correspond to the highest and lowest portion survival within each element category, and are not necessarily equal between elements (Note that lowest bone survivorship varies considerably between elements). Images represent composites of left and right elements in the assemblage.



Humerus

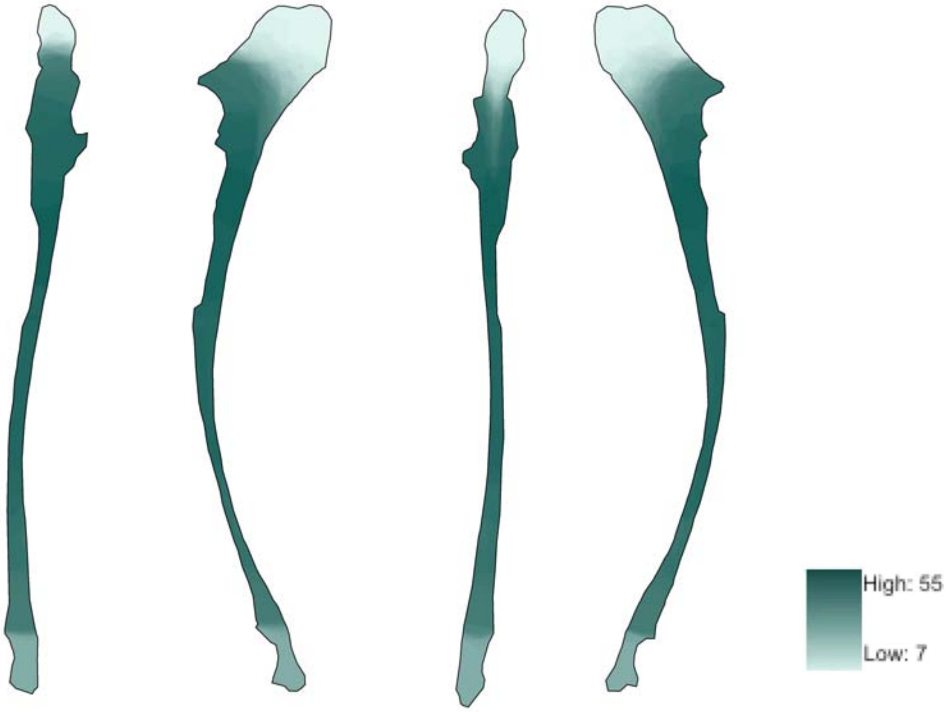
Figure 2.2 continued

Radius



Anterior Lateral Posterior Medial

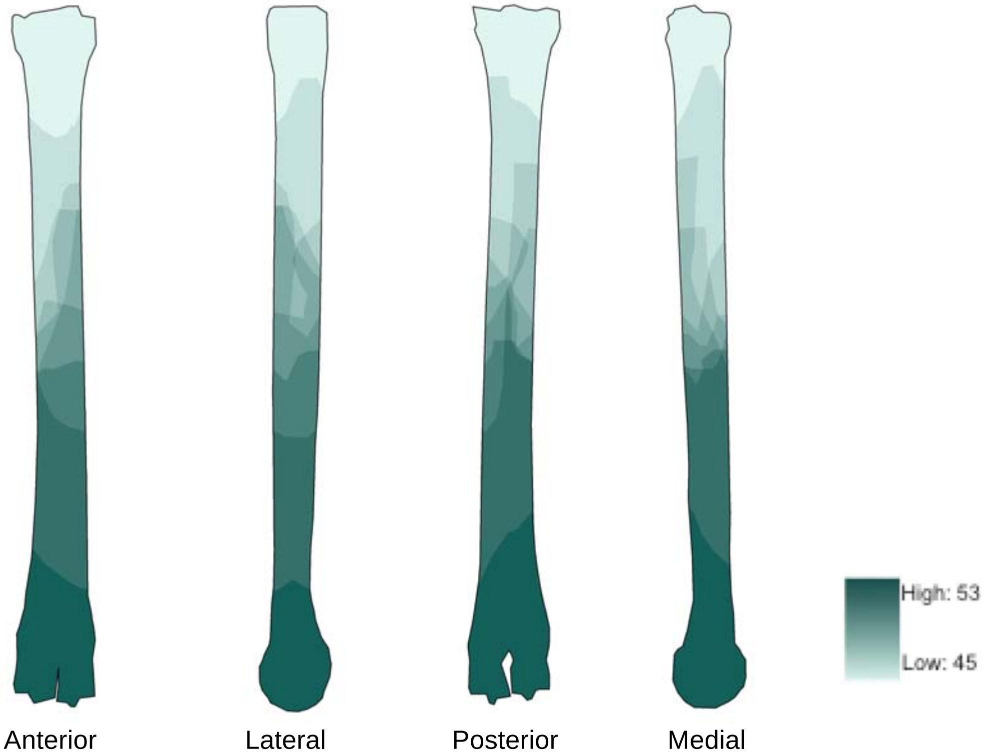
Ulna



Anterior Lateral Posterior Medial

Figure 2.2 continued

Metacarpal



Femur

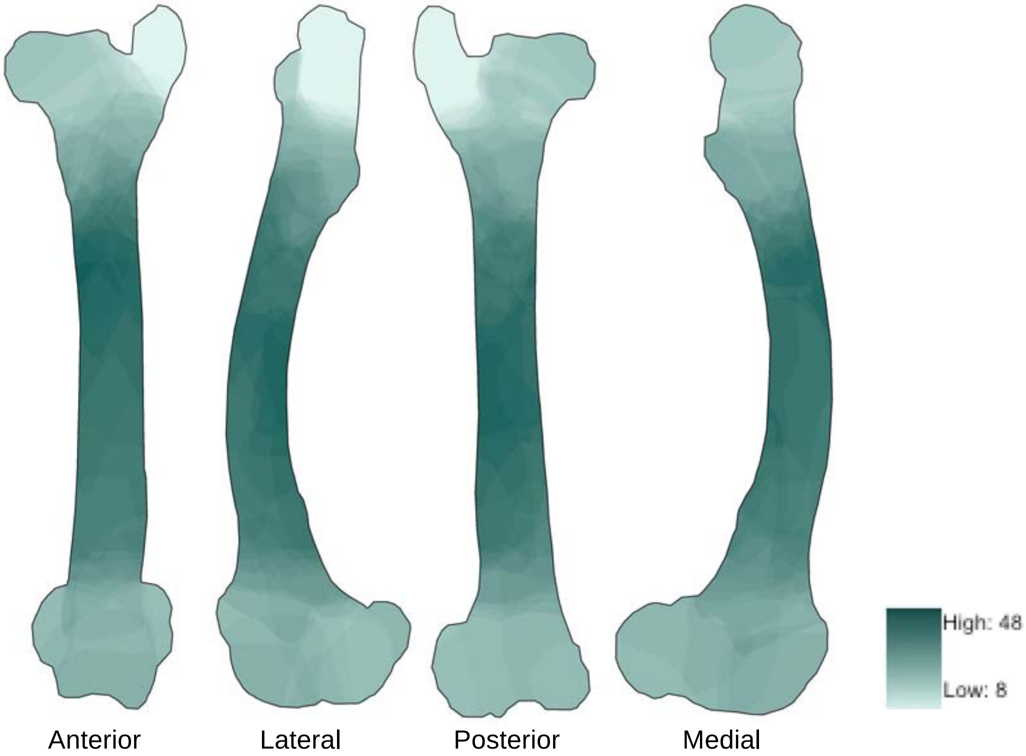
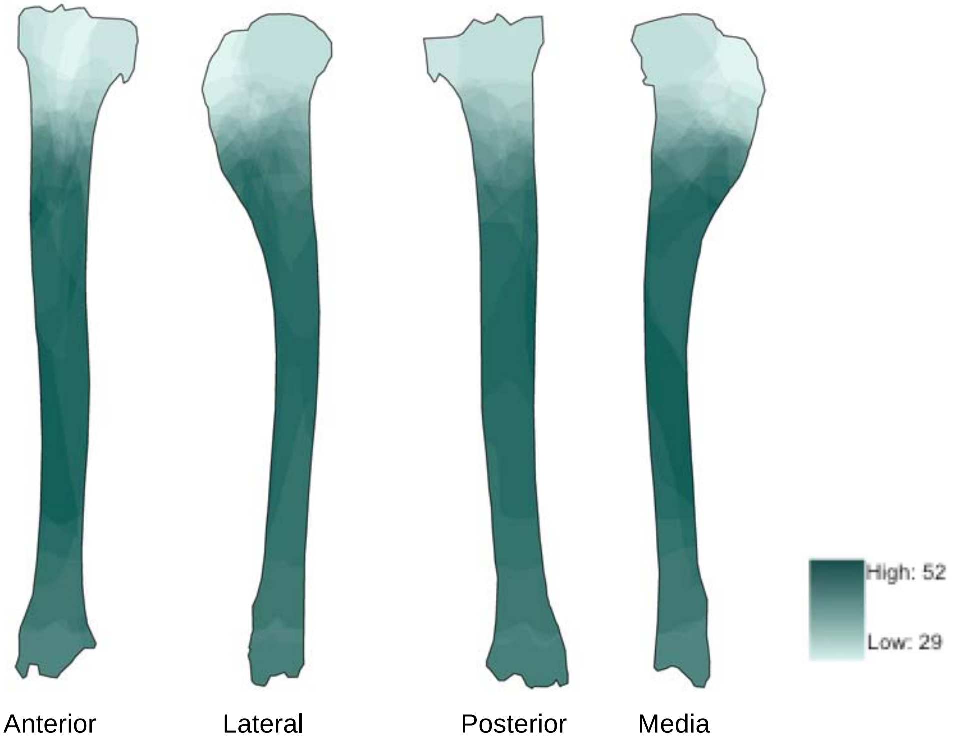
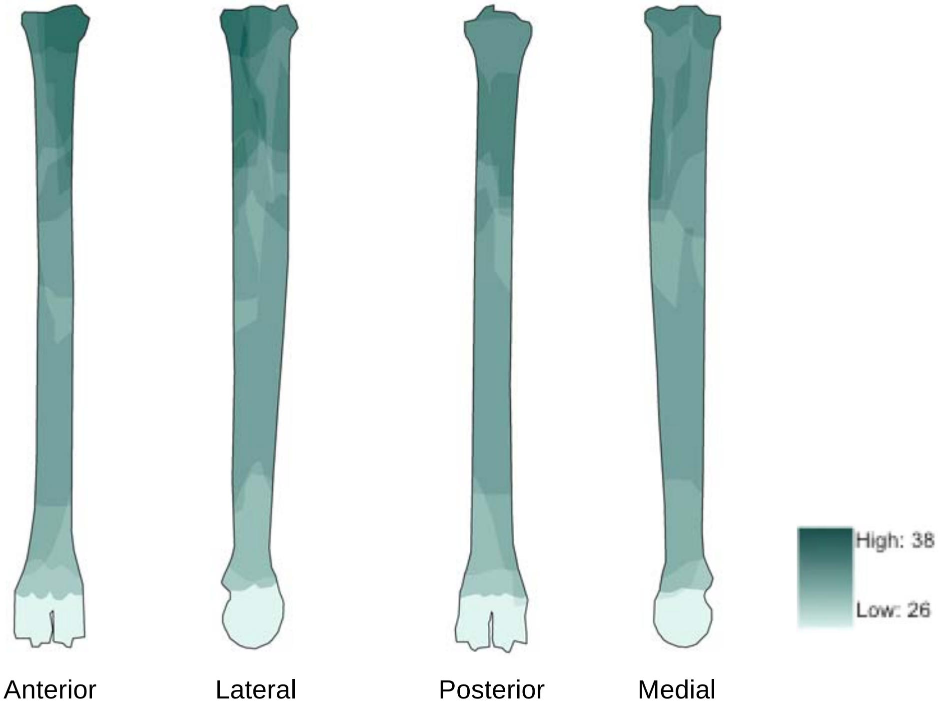


Figure 2.2 continued

Tibia



Metatarsal



Tooth Mark Cluster Analysis

Table 2.2 provides results of a GIS cluster analysis for tooth pits inflicted on small carcasses and Figure 2.3 illustrates tooth pit density results graphically. Tooth marks include both pits and scores. Areas of significant tooth mark clustering were identified on all elements. Typical patterns include tooth marking just under the humeral head on the lateral aspect as well as medially at the insertion for the teres major and the coracobrachialis muscles. On the distal end of the humerus, the medial epicondyle is also commonly tooth marked. Tooth marks are extremely common on the olecranon process of the ulna, and may also cluster on the distal

Table 2.2. GIS cluster analysis for tooth pits inflicted by large felids from CTR on size 1-2 carcasses. Analysis was performed on four aspects of all elements. The distance between each tooth pit and its nearest neighbor was measured. The nearest neighbor index (NNI) is the observed distance divided by the average expected distance in a hypothetical random distribution. If the NNI is less than 1, the pattern is considered clustered. If the NNI is greater than 1, the trend is toward dispersion. P-values indicating significant clustering of tooth pits appear in bold.

Element	Anterior	Lateral	Posterior	Medial
Humerus	Random	Clustered	Clustered	Clustered
NNI	0.82	0.71	0.65	0.75
p	0.136	**<0.001**	**<0.001**	**<0.001**
Radius	Clustered	Random	Dispersed	Clustered
NNI	0.41	1.18	1.28	0.71
p	**<0.001**	0.164	0.063	**0.048**
Ulna	n/a	Clustered	n/a	Clustered
NNI		0.58		0.83
p		**<0.001**		0.090
Metacarpal	Random	Clustered	Random	Clustered
NNI	0.86	0.56	0.94	0.50
p	0.120	**<0.001**	0.607	**<0.001**
Femur	Clustered	Clustered	Clustered	Clustered
NNI	0.81	0.75	0.83	0.82
p	**0.007**	**0.004**	**0.011**	**0.026**
Tibia	Dispersed	Clustered	Clustered	Clustered
NNI	1.40	0.77	0.64	0.65
p	0.030	**0.006**	**0.002**	**<0.001**
Metatarsal	Random	Clustered	Clustered	Clustered
NNI	0.89	0.59	0.72	0.77
p	0.233	**<0.001**	**0.009**	**0.011**

radius. Marks also significantly cluster on the proximal metacarpal. In terms of the hindlimb, tooth marking clusters occur at both the proximal and distal femoral epiphyses, as well as across the shaft anteriorly and posteriorly. The proximal tibia shows the largest cluster of all the limb bones, while the tibial shaft and distal end are rarely marked. Finally, the metatarsal preserves significant clusters at the distal end, but not proximally.

Figure 2.3. GIS density analysis results of tooth pit distribution performed on composite tooth pit plots for each element. Red areas indicate highest concentrations of tooth pits. n= number of specimens bearing tooth marks.

Humerus

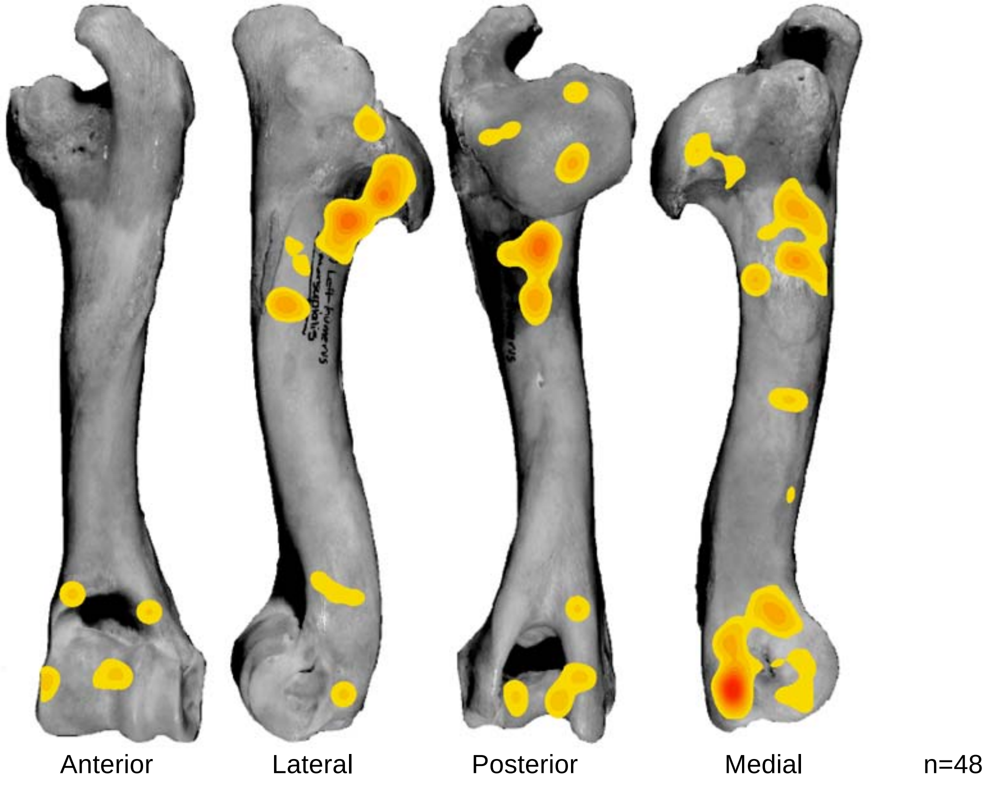
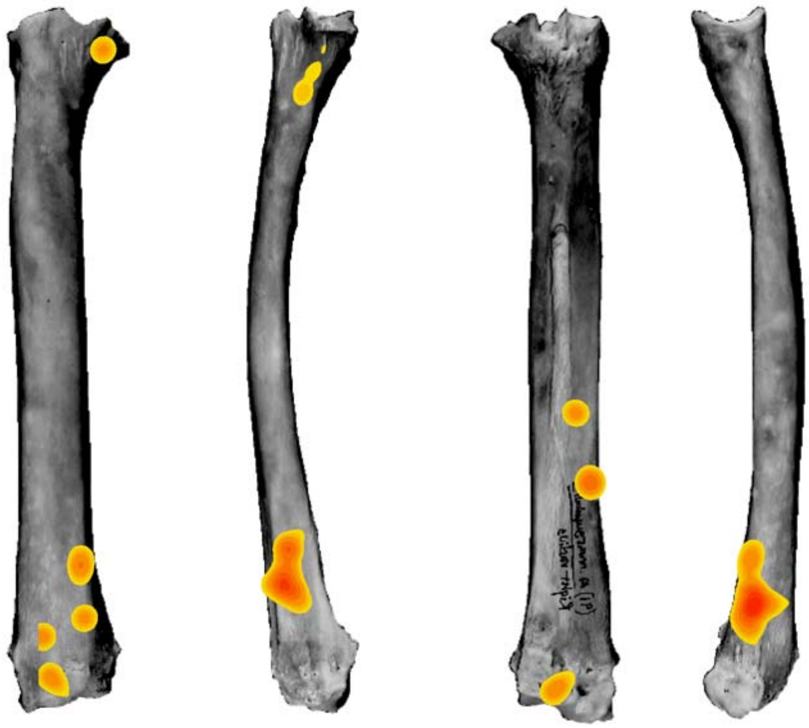


Figure 2.3 continued

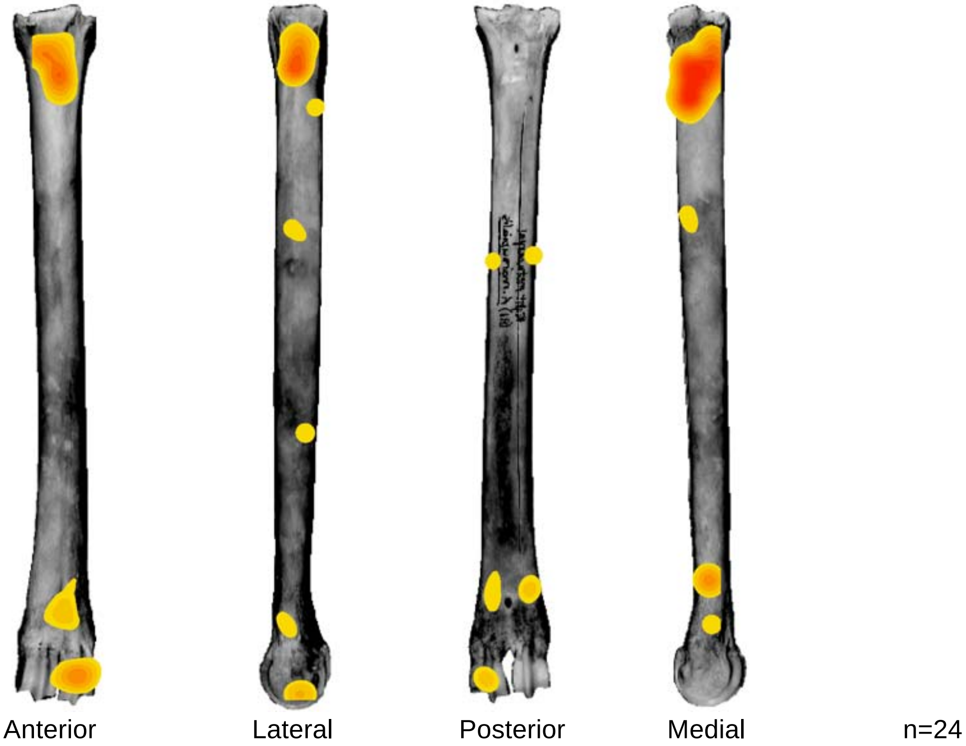
Radius



Ulna

Figure 2.3 continued

Metacarpal



Femur

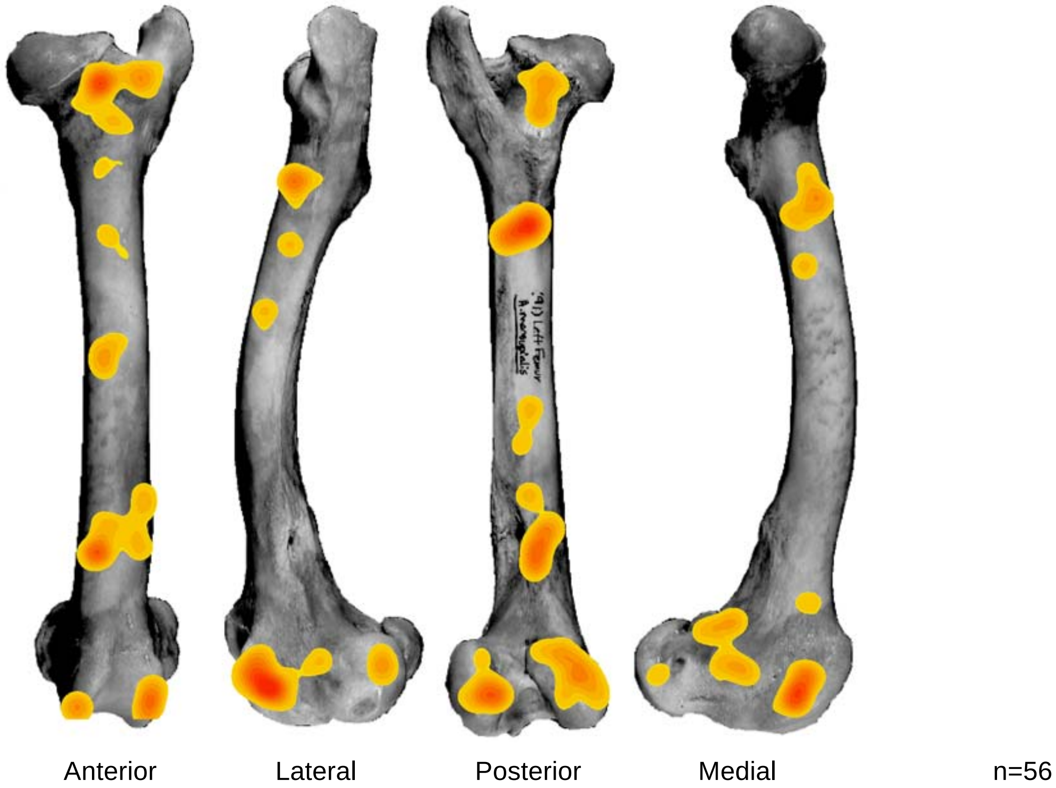


Figure 2.3 continued

Tibia

Metatarsal

TOOTH MARK FREQUENCIES

Among the large-bodied carnivores, felids are considered to be the most specialized flesh eaters, with dentition adapted for shearing meat rather than cracking bone (Van Valkenburgh 1989; Turner and Antón 1997). Because of this, it has been argued that felids should impart fewer tooth marks on bone compared to hyenas (Selvaggio 1994a; Domínguez-Rodrigo et al. 2007a). Results from this study of 435 limb bones confirm this. Overall, tooth mark frequencies on small (size 1 and 2) carcasses in my sample range from 55%-62% (Table 2.3, Figs. 2.4a-2.4b). A frequency of 64% was found in my larger (size 3) category. Experiments conducted by Blumenschine (1995) with wild spotted hyenas (*Crocuta crocuta*) show tooth marking frequencies of 71% for small carcasses and 87% for larger carcasses.

Faith (2007) has argued that long bone midshaft frequencies should be used instead of total NISP frequencies to interpret extent of carnivore damage in assemblages.
This controls for variation in tooth mark frequencies related to differential destruction of long bone epiphyses, which can be a problem particularly in hyena-modified assemblages. When examining tooth marking frequencies on the midshaft sections of size 1 and 2 bones in the CTR felid assemblage compared with Blumenschine's experimental spotted hyena-modified assemblage (Fig. 2.4a), hyenas - as expected -produce higher frequencies of tooth marks on midshafts. Hyenas also produce higher frequencies of tooth marks on the overall NISP, but the discrepancy is not as great as is seen in the midshafts. Size 1 specimens also show higher tooth mark frequencies than size 2 (Table 2.3). Compared to other studies of felid tooth marking frequencies, the CTR experiments with tigers and lions look most like observations made by Domínguez-Rodrigo et al. (2007a) of leopard and cheetah modified bones as far as both % overall NISP and % long bone midshafts with tooth marks. Pobiner's felid tooth mark

frequencies on small carcasses at Sweetwaters Game Reserve (SGR) are somewhat higher than my sample.

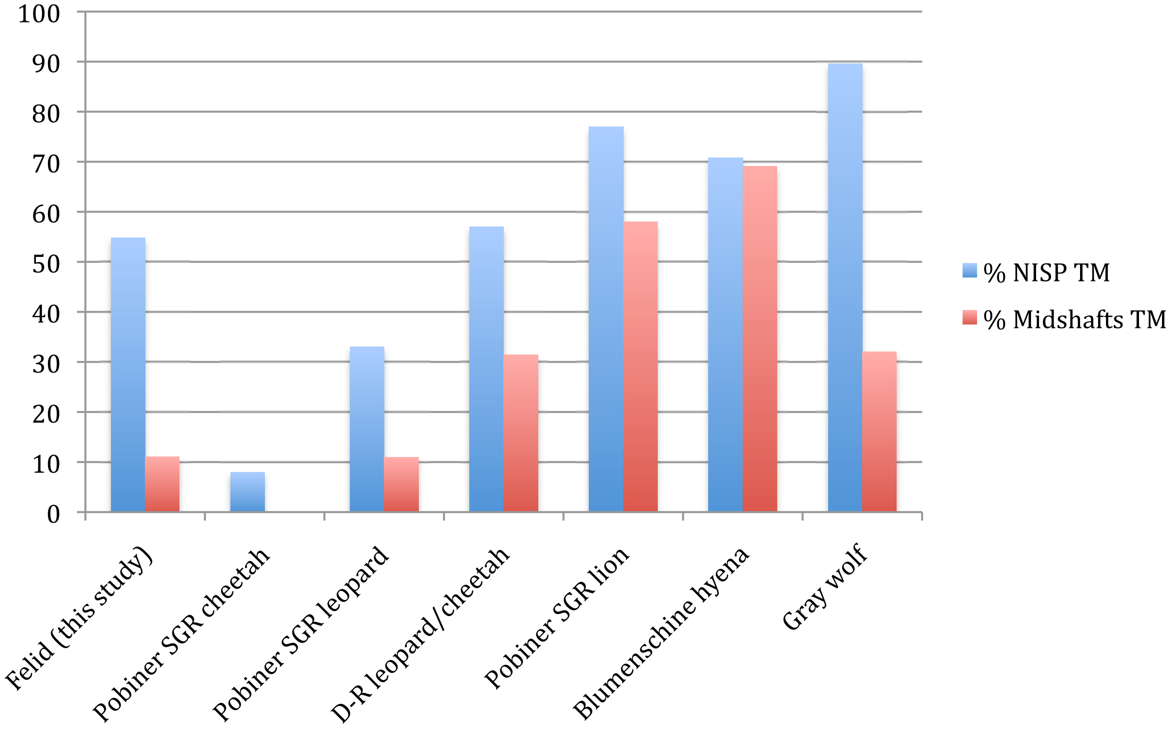
For the larger, size 3 and 4 carcasses, tooth mark frequencies for both midshafts and total NISP are also lower than in Blumenschine's hyena assemblage (Fig. 2.4b), though the difference is not as much as in the smaller carcasses. Total NISP tooth mark frequencies found in this study are similar to the other wild felid samples. Captive lion samples from Pobiner (2007) and Gidna (2013) are tooth marked at higher frequencies.

Table 2.3. Tooth mark frequency summary data for Carolina Tiger Rescue experiments (shaded) compared with reports of other felid- and hyaenid-modified assemblages. Lion and tiger samples are combined. Tooth marks include pits/punctures, and scores. Comparative data are from Pobiner (2007, Tables 4.2-4.6) for SGR (Sweetwaters Game Reserve) wild felids and NAO (Nairobi Animal Orphanage) captive felids. Domínguez-Rodrigo leopard/cheetah sample frequencies are derived from data in (Domínguez-Rodrigo et al. 2007b, Table 2 and data reported in text p. 261). Gidna et al. (2013) total NISP frequencies are calculated from Table 1 in their paper. Hyena tooth mark frequencies are from Blumenschine (1995) and Faith (2007). Large canid sample is from the large wolf group sample reported on in Chapter 1.Where cells are blank, data were unavailable.

	NISP	NISP TM	% TM	Midshaft NISP	Midshaft TM NISP	Midshaft % TM
Size 1/2 carcasses						
Felid (prey size 1)	21	13	**61.9**	21	6	**50**
Felid (prey size 2)	400	219	**54.8**	369	41	**11.1**
Pobiner SGR wild lion	70	54	**77**	43	25	**58**
Pobiner SGR wild leopard	12	4	**33**	9	1	**11**
Pobiner SGR wild cheetah	12	1	**8**	12	0	**0**
Domínguez-Rodrigo leopards & cheetahs	51	29	**57**	51	16	**31.4**
Blumenschine hyena			**70.8**			**69.1**
Faith hyena				238		**63.4**
Gray wolf	743	666	**89.6**	693	222	**32**
Size 3/4 Carcasses						
Tiger (prey size 3)	14	9	**64.3**	12	7	**58.3**
Pobiner SGR wild lion	94	48	**51**	66	22	**33**
Pobiner NAO captive lion	22	17	**77**	21	6	**29**
Gidna wild lion	112	60	**53.6**			
Gidna captive lion	60	50	**83.3**			
Pobiner NAO captive cheetah	16	6	**38**	11	2	**18**
Blumenschine hyena			**86.5**			**87.7**
Faith hyena				174		**75.3**
Gray wolf	22	17	**77.3**	22	5	**22.7**

Figure 2.4. Comparison of tooth mark frequencies in Carolina Tiger Rescue experiments with other assemblages modified by felids, hyenas and gray wolves. Data are from Table 2.3.

(a) Size 1-2 carcasses



(b) Size class 3-4 carcasses

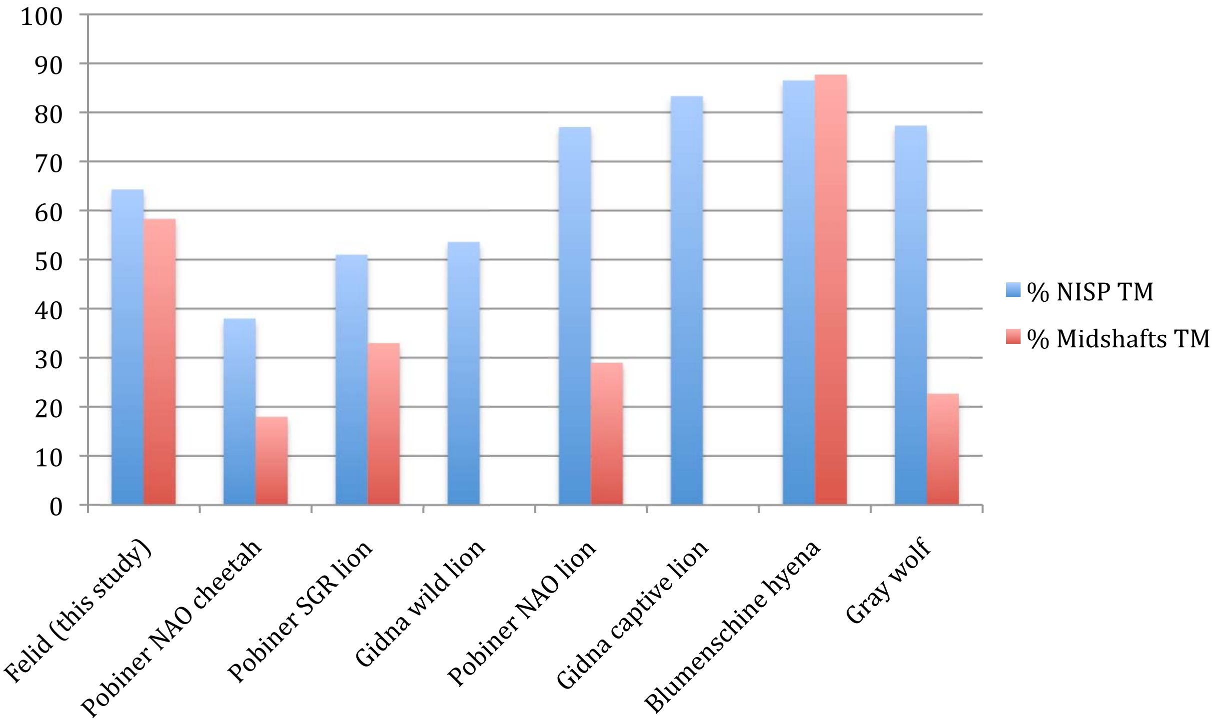


Table 2.4 illustrates tooth mark frequencies from these experiments broken down by bone portion and compared with other studies. The femur, tibia, and humerus show higher frequencies of tooth marking than other limb elements. These same elements were also highly tooth marked in Pobiner's lion experiments.

GROSS BONE DAMAGE

Coding Gross Bone Damage

Gross bone damage data were collected on all limb bones in this study and on a subset of the girdle bones using the coding convention developed by Pobiner and Blumenschine (2003) and expanded in Pobiner (2007). Table 2.5 outlines the coding convention as applied to this assemblage, which is adapted from Pobiner (2007, Table 3.2). I use the same damage level definitions as Pobiner, but do not include axial elements or podials other than the metapodials. I also separate metatarsals from metacarpals in this analysis in order identify potential differences in damage patterns between these elements.

Figures 2.5 illustrates average gross bone damage stages for hindimbs and forelimbs of small carcasses. I report average rather than median, as Pobiner's study reported because of the high variation in the range of damage categories in my sample. Within almost every bone portion category, there is a range from 0 (no damage) to 4 (maximum damage). Therefore, in this sample the average damage pattern is more revealing.

The bulk of my experimental sample consisted of size class 2 carcasses, but I did have the opportunity to conduct two additional experiments with larger sized limbs with differing flesh distributions. Gross bone damage data for these size class 3 experiments are presented for each experiment individually, and will be discussed separately.

Table 2.4. Tooth mark frequencies (expressed as %) inflicted by felids on small carcasses in this study (shaded) compared with Pobiner's (2007) study of wild felids at Sweetwaters Game Reserve (SGR). Tooth mark frequencies are separated by bone portion. Pobiner's data include size 1 and 2 combined. NISP = sample size for each experiment.

	Proximal epi	Proximal shaft	Midshaft	Distal shaft	Distal epi	Total % TM	Total NISP
HUMERUS							
Felid size 1	0	0	0	0	0	0	1
Felid size 2	62	51	10	17	34	71	66
SGR Lion	100	83	67	50	n/a	81	11
SGR Leopard	n/a	n/a	n/a	n/a	n/a	n/a	0
SGR Cheetah	0	0	0	0	0	0	2
RADIUS							
Felid size 1	0	25	0	0	0	25	4
Felid size 2	3.8	10.7	8.5	17.9	12.8	33.3	60
SGR Lion	25	100	75	67	0	100	3
SGR Leopard	n/a	n/a	n/a	n/a	n/a	n/a	0
SGR Cheetah	0	0	0	0	0	0	2
METACARPAL							
Felid size 1	0	0	33.3	0	0	33.3	6
Felid size 2	6.8	35.4	6.1	14	14	44	50
SGR Lion	0	44	30	50	29	36	14
SGR Leopard	n/a	n/a	n/a	n/a	n/a	n/a	0
SGR Cheetah	0	0	0	0	0	0	2
FEMUR							
Felid size 1	0	20	40	25	100	100	6
Felid size 2	58.8	50	24.6	24.5	45.5	76.5	68
SGR Lion	n/a	100	70	89	100	92	13
SGR Leopard	50	33	33	33	75	100	3
SGR Cheetah	0	0	0	0	50	50	2
TIBIA							
Felid size 1	0	33.3	33.3	33.3	0	66.7	3
Felid size 2	42.9	40	15.1	11.3	2	60.7	56
SGR Lion	n/a	100	73	73	17	92	13
SGR Leopard	0	33	0	33	0	25	4
SGR Cheetah	0	0	0	0	0	0	2
METATARSAL							
Felid size 1	50	50	50	0	0	50	2
Felid size 2	7.9	15.4	8.3	31.4	11.1	41.5	41
SGR Lion	25	83	40	86	100	100	6
SGR Leopard	0	0	0	0	0	0	5
SGR Cheetah	0	0	0	0	0	0	2

Table 2.5. Coding convention for gross bone damage levels on specific bone portions. Damage levels were recorded from 0-4, where damage level 0 = no visible damage, and damage level 1 = tooth marks only. Damage levels 2, 3, and 4 are defined below. This coding convention is adapted from Pobiner (2007, Table 3.2). Portion definitions (in footnotes) originally defined by Pobiner (2007).

	Damage Level 2	**Damage Level 3**	**Damage Level 4**
HINDQUARTER			
Greater Trochanter	superior margin gnawed	1/2 destroyed	destroyed to base
Femur Head	some cancellous bone exposed	partially destroyed	completely destroyed
Prox. Femur[1]	marginal gnawing	partially destroyed	completely destroyed to prox. shaft
Femur Shaft	gnawing on prox. and dist. ends of intact shaft, missing epiphyses	shaft partially fragmented	shaft heavily fragmented/destroyed
Distal Femur – Patellar Groove	marginally gnawed	partially destroyed	destroyed to dist. shaft
Distal Femur – Condyles	marginally gnawed	partially destroyed	destroyed to dist. shaft
Prox. Tibia	tibia crest gnawed	articular surfaces also gnawed	destroyed to prox. shaft
Tibia Shaft	gnawing on prox. and dist. ends of intact shaft, missing epiphyses	shaft partially fragmented	shaft heavily fragmented/destroyed
Distal Tibia	cancellous bone exposed on dist. articular areas	destruction of some part of dist. epiphysis	destroyed to dist. shaft
Iliac Blade	crest gnawed	1/2 destroyed	destroyed to acetabulum
Posterior Innominate[2]	gnawing on caudal margin of pubis and/or ischial tuberosity	1/2 destroyed	completely destroyed
Pubic Region[3]	gnawing on cranial margin of pubic symphysis	destruction of some part of region	completely destroyed
Ischial/Pubic Base[4]	gnawing on margin of posterior projection of ischium	posterior projections of ischium 1/2 destroyed	destroyed to superior ischium
Acetabulum	margins gnawed	partially destroyed	only fragments remain
Prox. Metatarsal	marginal gnawing	partially destroyed	fragments only
Metatarsal Shaft	gnawing on prox. and dist. ends of intact shaft, missing epiphyses	shaft partially fragmented	shaft heavily fragmented/destroyed
Distal Metatarsal	marginal gnawing (small amount of cancellous bone exposed, esp. on dist. condyles)	partially destroyed (e.g., one condyle), some articular area still present	completely destroyed up to near-epiphyses
FOREQUARTER			
Scapular Blade[5]	superior margin gnawed (and cartilage extension destroyed)	up to 1/2 of blade destroyed	blade including spine destroyed; only neck and glenoid remain
Scapular Glenoid	marginally gnawed acromium	gnawing along margins of glenoid fossa	only fragments remaining
Prox. Humerus	gnawing on head +/or tubercles	at least one tubercle destroyed	head also destroyed
Humerus Shaft	gnawing on prox. and dist. ends of intact shaft, missing epiphyses	shaft partially fragmented	shaft heavily fragmented/destroyed

Table 2.5 continued

Distal Humerus	marginal gnawing on epiphysis	partial epiphyseal destruction	epiphysis completely destroyed
Olecranon Process (Ulna)	marginal gnawing with some cancellous bone exposed; articular area still intact	partial destruction	olecranon process completely destroyed
Prox. Radio-Ulna	marginal gnawing on/around articular surface	partial destruction	epiphysis completely destroyed
Radio-Ulna Shaft	gnawing on prox. and dist. ends of intact shaft, missing epiphyses	shaft partially fragmented	shaft heavily fragmented/destroyed
Distal Radio-Ulna	marginal gnawing on/around articular surface	partial destruction	epiphysis completely destroyed
Prox. Metacarpal	marginal gnawing	partially destroyed	fragments only
Metacarpal Shaft	gnawing on prox. and dist. ends of intact shaft, missing epiphyses	shaft partially fragmented	shaft heavily fragmented/ destroyed
Distal Metacarpal	marginal gnawing (small amount of cancellous bone exposed, esp. on dist. condyles)	partially destroyed (e.g. one condyle), some articular area still present	completely destroyed up to near-epiphyses

[1] defined as all epiphyseal areas excluding greater trochanter and head
[2] defined as region posterior of iliac blade beginning at branch, including ischial tuberosity, to iliopubic ramus
[3] defined as pubis and pubic symphysis (t-shaped area)
[4] defined as all regions posterior of acetabulum and obturator foramen
[5] includes scapular spine

Gross Bone Damage to Size 1-2 Carcasses

Figures 2.5a-b illustrate damage levels for size 1 and 2 carcasses (data from Table 2.6) The highest damage levels are seen on the scapular blade, proximal humerus, and olecranon process of the ulna, and moderate degrees of damage are seen on the proximal and distal femora. These patterns largely reflect patterns of preservation identified in the GIS image analysis, but particularly common occurrences of puncturing or furrowing are identified here as well.

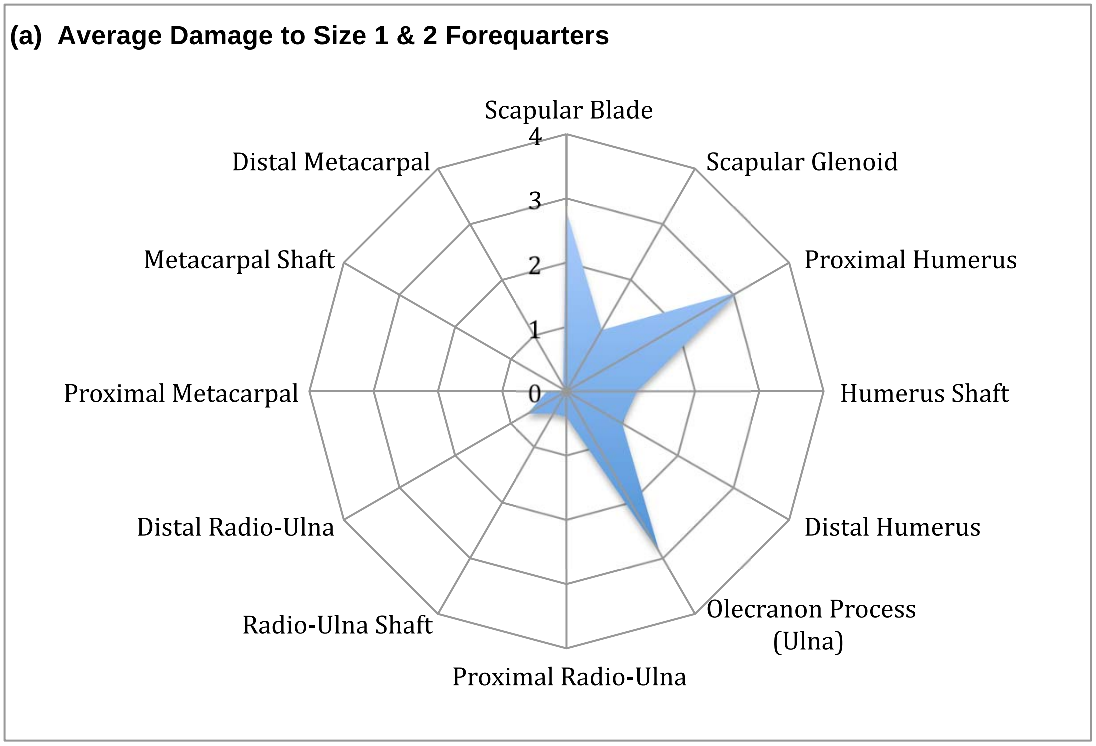
Scapula

In this sample, the scapular blade was often crushed to varying degrees, similar to what Pobiner (2007) found on size 1 and 2 prey damaged by lions in the wild. Sometimes tooth punctures pierced the blade. The scapular neck was normally intact, but commonly tooth marked. The glenoid fossa was typically untouched. Figure 2.6 illustrates the typical range of damage to scapulae in my experiments.

Table 2.6. Summary data on gross bone damage levels for each bone portion in Carolina Tiger Rescue experiments. Description of damage levels are listed in Table 2.5. Damage level given is the mode (the most common damage stage) followed by the average, followed by the range of damage: (mode / average / min-max). n = number of specimens examined for each element portion (not the number of carcasses). Where no data are available, cells are left blank. Where sample size is too small to calculate a mode or average, only the range of damage is reported.

	Size 1/2		**Size 3**	
Skeletal Element/Portion	n	Gross Bone Damage Level	n	Gross Bone Damage Level
HINDLIMB				
Greater Trochanter	46	4 / 2.6 / 0-4		
Femur Head	45	4 / 2.3 / 0-4		
Femur Shaft	47	0 /1.4 / 0-4		
Distal Femur – Patellar Groove	44	4 / 2.0 / 0-4		
Distal Femur – Condyles	41	4 / 2.0 / 0-4		
Patella				
Prox. Tibia	50	0 / 1.8 / 0-4	1	4-4
Tibia Shaft	50	0 / 0.8 / 0-4	1	1-1
Distal Tibia	50	0 / 0.4 / 0-4	1	1-1
Iliac Blade	25	3 / 2.5 / 1-4		
Posterior Innominate	25	2 / 2.2 / 0-4		
Pubic Region	25	0 / 1.7 / 0-4		
Ischial/Pubic Base	25	2 / 2.2 / 0-4		
Acetabulum	25	0 / 0.3 / 0-3		
Prox. Metatarsal	56	0 / 0.3 / 0-4		
Metatarsal Shaft	56	0 / 0.5 / 0-4		
Distal Metatarsal	55	0 / 0.8 / 0-4		
FORELIMB				
Scapular Blade	27	3 / 2.8 / 0-4		
Scapular Glenoid	28	0 / 1.1 / 0-4		
Prox. Humerus	59	4 / 3.1 / 0-4	2	4-4
Humerus Shaft	60	0 / 1.1 / 0-4	2	3-3
Distal Humerus	57	0 / 1.0 / 0-4	2	3-4
Olecranon Process (Ulna)	55	3 / 2.9 / 0-4		
Prox. Radio-Ulna	61	0 / 0.4 / 0-4	2	4-4
Radio-Ulna Shaft	61	0 / 0.4 / 0-4	2	0-1
Distal Radio-Ulna	61	0 / 0.7 / 0-4	3	
Prox. Metacarpal	43	0 / 0.3 / 0-4	3	0 / 0.3 / 0-1
Metacarpal Shaft	43	0 / 0 / 0-0	3	0 / 0 / 0-0
Distal Metacarpal	43	0 / 0.1 / 0-1		0 / 0 / 0-0

Figure 2.5. Radial diagrams showing average bone damage level for size 1 and 2 carcasses. (a) forelimbs and (b) hindlimbs. Damage level definitions are listed in Table 2.5. Data (including number of specimens in each element category) are from Table 2.6. n ranges from 25-51 specimens.


(a) Average Damage to Size 1 & 2 Forequarters

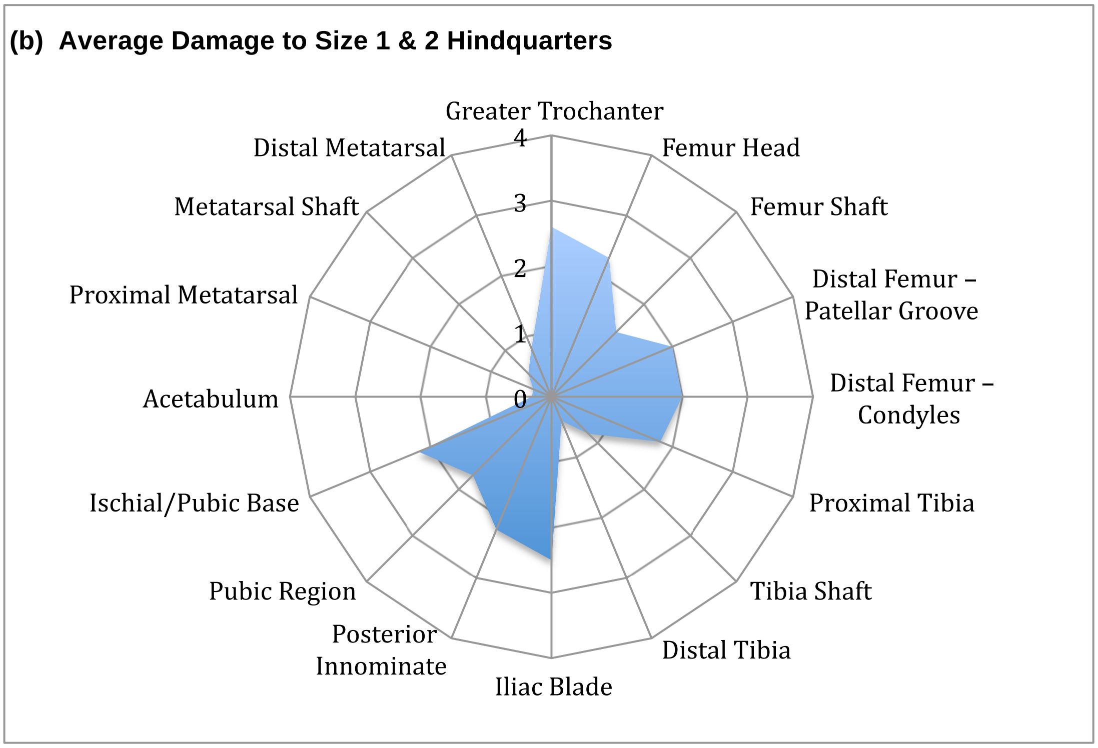

(b) Average Damage to Size 1 & 2 Hindquarters

Figure 2.6. Range of damage seen on size 1&2 scapulae from CTR. Dorsal view, left side. Note progressive destruction of blade.

Humerus

The proximal end of the humerus shows intensive damage in my experiments (Fig. 2.8a). Domínguez-Rodrigo and colleagues have observed that in Brain's (1981) leopard-modified experiments, the proximal humerus is often furrowed, and that felids "impart serious damage on the caudal side of the distal humeral epicondyles, leaving the frontal facet of the epicondyles intact" (Domínguez-Rodrigo et al. 2007a:150). Moreover, they argue that felid gnawing is most prevalent on the medial side of the caudal epicondyle, and that this contrasts damage produced by hyaenids, where epiphyseal deletion begins with the lateral epicondyle (Domínguez-Rodrigo 2009). Brain's (1981) experiments, which Domínguez-Rodrigo's observations are based on, included 6 small bovids consumed by leopards, and 1 baboon consumed by a cheetah (see description in Domínguez-Rodrigo et al. 2007b). The data presented here, with a sample size of 56 individual humeri of the same size class do not show damage to the humeral epicondyles to be as common as Domínguez-Rodrigo and colleagues have suggested. Figure 2.7 shows the more common range of humeral damage seen in the CTR experimental assemblage. Epicondyles are damaged in many cases (Fig 2.8b), and slightly more on the medial side, but not commonly enough to warrant identifying this alone as a felid-specific pattern. My canid-modified experimental sample in fact shows the pattern Domínguez-Rodrigo and colleagues described a bit more clearly than the CTR sample (see Chapter 1).

Radio-Ulna

As Pobiner (2007) also observed in her experiments, felids nearly always at least minimally damage the ulnar olecranon process (Fig 2.9). The radius normally remains intact, with minimal damage (Fig.2.10). There may be minimal tooth marking on the distal epiphysis. The specimen on the far right in Fig 2.10 is the greatest extent of the damage seen, and is atypical in this sample

Figure 2.7. Range of damage seen on size 1&2 humeri from CTR. Posterior view, left side.

Figure 2.8. Common damage seen on size 1&2 humeri from CTR. (a) Furrowing and puncture on proximal humerus (posterior view, left side, medial aspect). (b) Damage to posterior lateral epicondyle.

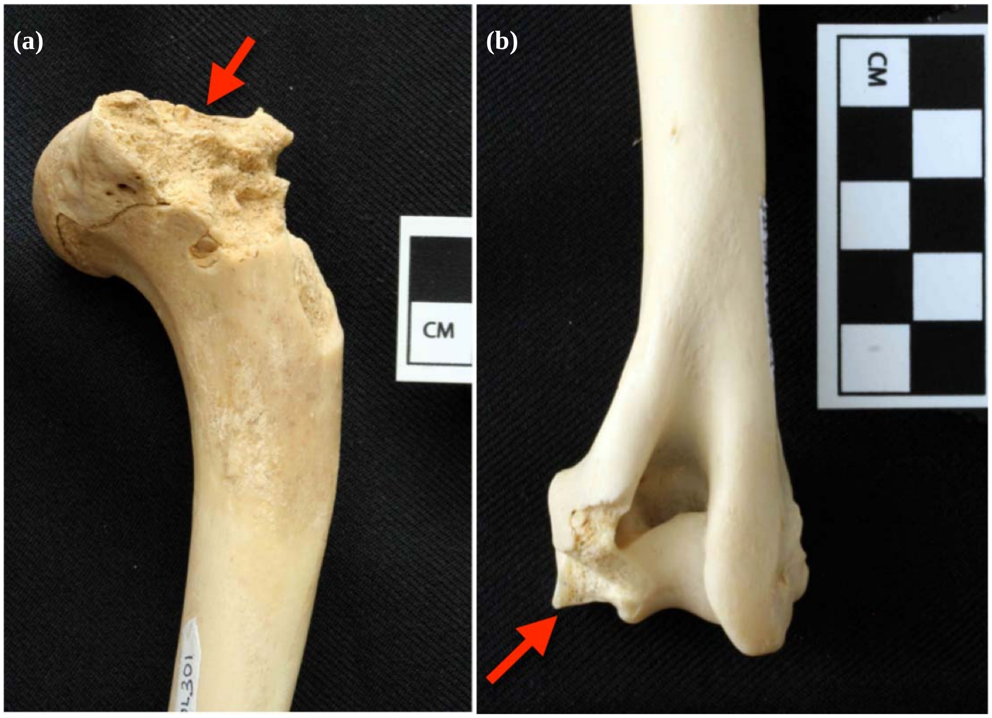


Figure 2.9. **Range of damage seen on size 1&2 ulnae from CTR.** Note damage to olecranon processes. Left side, lateral aspect.

Figure 2.10. Range of damage seen on size 1&2 radii from CTR. Left side, anterior aspect. Specimen on the far right is atypical.

Metacarpal

The metacarpals typically do not show signs of gross bone damage. When they are damaged, the proximal end may bear tooth marks, or may be partially destroyed. The distal end is always intact.

Femur

Both the proximal and distal ends of the femur display gross bone damage with some destruction of the epiphyses (Fig 2.11). Furrowing is visible particularly on the distal epiphyses, which often also show punctures on the medial or lateral surface of the condyles (Fig 2.12). Felids may also damage the shaft to some degree, although shafts in the CTR experiments were not damaged to same extent as in Pobiner's experiments. Pobiner's study also included the patella, which I did not examine here. However, I can note from non-quantified observations that the patellae were either not recovered in these experiments (and presumably destroyed) or recovered complete and undamaged. This is in contrast to Pobiner's study, which showed high levels of damage to the patellae of both small and large carcasses by lions.

Figure 2.11. Range of damage seen on size 1&2 femora from CTR. Left side, anterior view.

Figure 2.12. Common damage to distal femur on size 1&2 carcasses from CTR. Lateral aspect. Arrows indicate furrowing of the lateral condyle and tooth puncture.

Tibia

Damage to the distal femur extends across the joint to the proximal tibia. My observations are in line with those of Domínguez-Rodrigo et al. (2007a) who show that the proximal end of the tibia may be severely damaged, while the shaft and distal end remain intact (Fig 2.13). In only 2% of my experiments was the distal epiphysis tooth marked, but in those cases damage was severe. Damage to the distal end was documented in Pobiner's experiments more commonly.

Metatarsal

Metatarsals are typically undamaged (Fig 2.14), and in fact were most often still encased in hide at the end of the experiments. When damaged, they seem to be gnawed from the distal end upward, which is opposite the pattern seen in the metacarpals.

Figure 2.13. Range of damage seen on size 1&2 tibiae from CTR. Right side, anterior view.

Figure 2.14. Range of damage seen on size 1&2 metatarsals from CTR. Left side, anterior view.

Innominate

All parts of the innominate are normally tooth marked, and may be heavily fragmented (Fig 2.15). The iliac blade and posterior portion of the innominate are particularly prone to destruction. The acetabulum is always intact, and rarely shows tooth marking.

Vertebrae

Gross bone damage to the vertebrae is not quantified here, but in almost every case vertebrae were preserved. Normally they were still articulated and held together by tendon after the experiments. Tooth marks were not common, but when present, they occurred on the ends of the apophyses. The centra always remained intact. Tooth marking on the apophyses is a pattern that Domínguez-Rodrigo et al. (2007a) argue is diagnostic of felid damage, because hyenas tend to completely destroy vertebra of smaller prey animals.

Figure 2.15. Range of damage seen on size 1&2 pelves from CTR. Left side, lateral aspect.

Gross Bone Damage to Size 3 Carcasses - Fleshed vs. Defleshed limbs

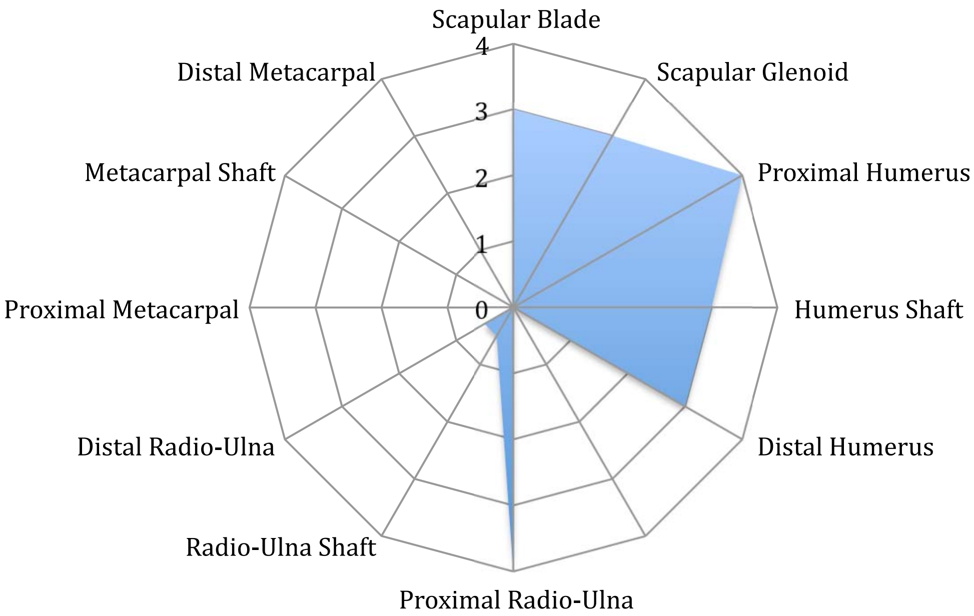
I had the opportunity to conduct two additional experiments with larger-sized limbs with different flesh distributions. Experiment number 40 consisted of three fully fleshed large calf limbs (two front and one hind) fed to a group of three tigers. Experiment 15 consisted of one cow forelimb defleshed using a metal knife and fed to a single tiger.

Fleshed limbs (Experiment 40)

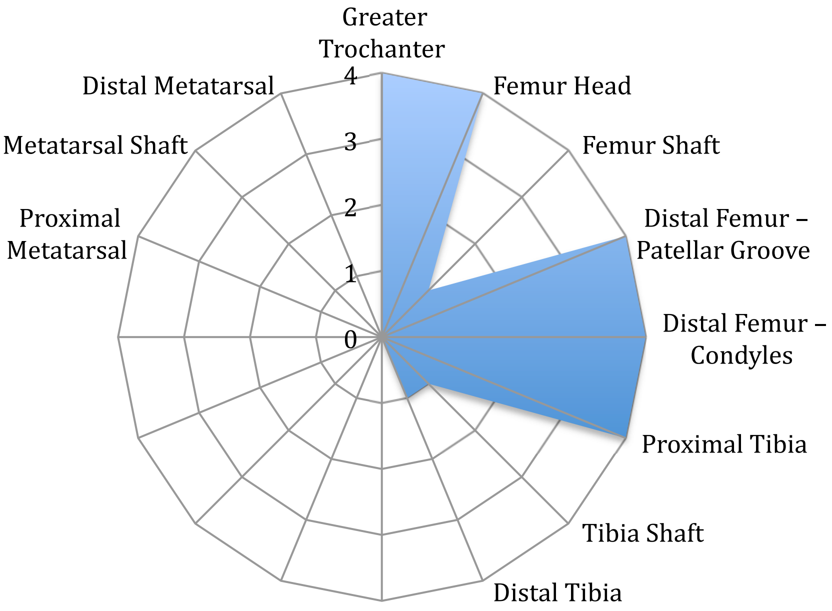
In the experiment with fleshed limbs, the tigers quite heavily damaged the humerus along with the proximal radio-ulna (Fig. 2.16a). The scapula is also heavily damaged, with part of the blade gnawed away, and a large tooth puncture on the scapular neck (Fig. 2.17a). This pattern is similar to that documented in the CTR size 1 and 2 experiments, as well as that identified by Domínguez-Rodrigo et al. (2007a, Fig. 111) in the FLK North 3 assemblage, which they attribute

Figure 2.16. Radial diagrams showing average bone damage level for size 3 limbs from Experiment 40. This experiment consisted of 3 large calf limbs (2 front and 1 hind) fed to a group of 3 tigers. Where no data were available bone portion labels are not shown on the diagram.

(a) Average Damage to Size 3 Forelimb – Experiment 40



(b) Damage to Size 3 Hindlimb – Experiment 40



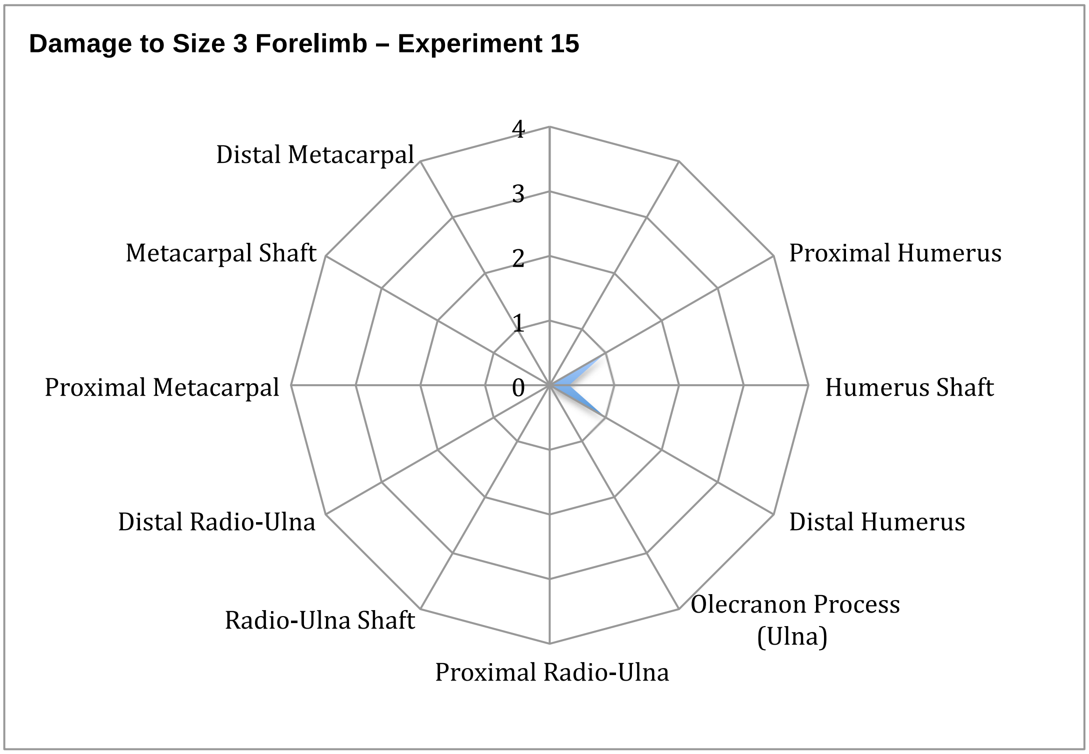
to felids. The metacarpals from experiment 40 were intact, but one displays a large tooth puncture at the proximal end (Fig. 2.17b). The hindlimb in this experiment (Fig. 2.16b) showed severe damage to the proximal and distal femur, but minimal damage to the femoral shaft. The proximal tibia was also severely damaged. The metatarsal was undamaged.

Defleshed limbs (Experiment 15)

In the experiment with the defleshed forelimb, there is almost no gross bone damage (Fig. 2.18). All bones were recovered after the experiment was complete, but the only visible damage was tooth marking on the proximal and distal humerus. This pattern might be expected given that felids are flesh specialists, and so are less likely to be interested in defleshed bones.

Figure 2.17. (a) Dorsal view of size 3 scapula #614 from Experiment 40 (fleshed whole limbs fed to tigers. (b) Anterior view of size 3 metacarpal #601 also from Experiment 40. Arrows indicate tooth punctures on these elements.

Figure 2.18. Radial diagrams showing average bone damage level for size 3 limbs from Experiment 15. This experiment consisted of one cow forelimb fed to a single tiger, however the limb had been previously partially defleshed, and may not be an accurate representation of typical damage levels. Where no data were available bone portion labels are not shown on the diagram.

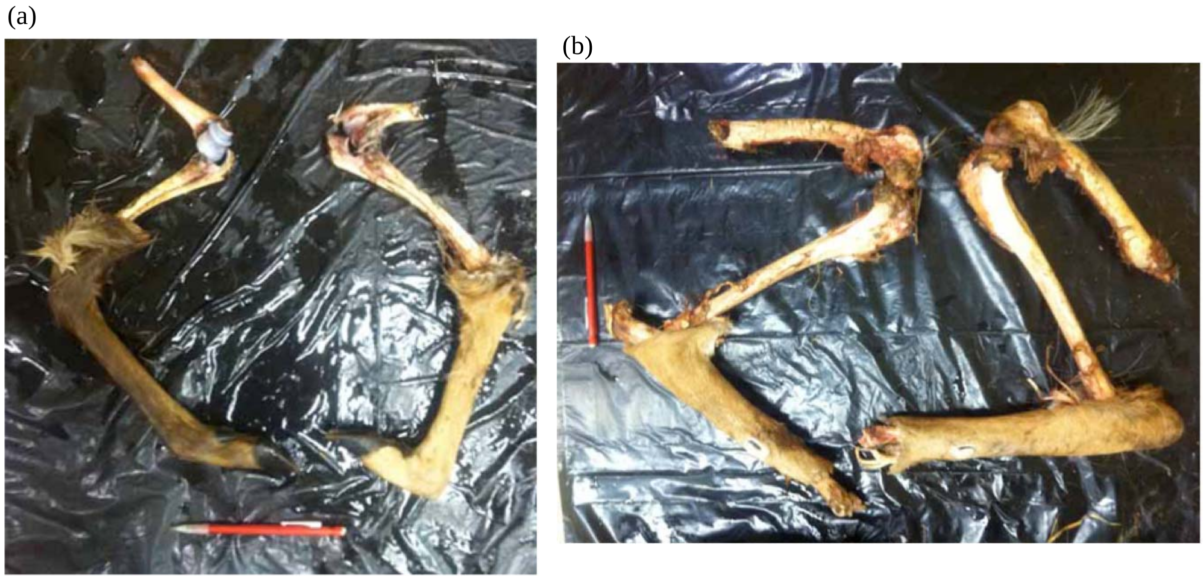


FLESH AVAILABILITY

In order to assess whether scavenging from felid kills might have been a viable strategy for early hominins, Domínguez-Rodrigo (1999) conducted a study of flesh availability on wildebeest and zebra carcasses consumed by lions. His idea was that if scraps of flesh remained after lion consumption, scavenging felid kills could be a reliable food source. His study found that lions typically thoroughly consume flesh from carcasses, leaving little behind. Pobiner (2007) conducted a similar study which documented a much larger amount of scavengable flesh for size 3 and 4 lion kills than in Domínguez-Rodrigo’s study. As these previous studies have yielded conflicting results, I have added data to this sample by analyzing flesh distribution on 79 complete limbs from small (mostly size 2) carcasses from the CTR experiments.

I assessed presence or absence of bulk flesh and flesh scraps on complete limbs, and categorized each limb as either preserving bulk flesh, flesh scraps, or as defleshed (Fig. 2.19). Bulk flesh on limbs is defined following Domínguez-Rodrigo (1999) as more than 10% of the original flesh mass present. Flesh scraps are defined following Pobiner (2007) where bones with flesh scraps remaining had less than 10% of their original flesh mass present. Scraps were less than the size of an average human’s palm, but larger than 2-3 cm. This definition of flesh scrap is intended to identify those scraps that would have been worth scavenging for hominins.

Fig. 2.19. Photos illustrating typical felid defleshing of limbs in CTR experiments. Note almost no flesh remains on upper and intermediate limb elements, but metapodials are still fleshed. (a) forelimbs, (b) hindlimbs. Arrow pointing to flesh scrap.



I found that 62% of the limbs in my study were completely defleshed, while only 3% preserved any bulk flesh (Table 2.7). This is similar to the percentage of defleshed limbs Domínguez-Rodrigo found in his study of size 3 carcasses (59.3%). My values are consistent with what Pobiner found for small carcasses (she reports 44% of size 1 and 2 carcasses fed on by lions had some flesh remaining). However, Pobiner found a much higher frequency of flesh remaining on larger, size 3 and 4 carcasses fed on by lions (95%). The variation seen in these studies perhaps reflects the higher likelihood of lions leaving more flesh scraps on larger carcasses, while they more fully consume the smaller carcasses.

Table 2.7. Distribution of bulk flesh and flesh scraps in CTR limbs

Total n limbs	Limbs with bulk flesh	Limbs with flesh scraps	Completely defleshed limbs
79	2 (3%)	30 (38%)	49 (62%)

Table 2.8. Distribution of flesh scraps by bone portion in CTR limbs

	Proximal	Midshaft	Distal
Upper	6/46 (13%)	1/66 (1.5%)	12/64 (18.8%)
Intermediate	8/76 (10.5%)	7/76 (9.2%)	15/76 (19.7%)
Lower	unmodified	unmodified	unmodified

Fraction represents number of bone portions preserving flesh scraps / number of bone portions in that category represented in the sample

In order to characterize the anatomical distribution of flesh scraps, I also recorded the distribution of scraps by bone category following the methodology of Domínguez-Rodrigo (1999) (Table 2.8). Upper (humerus, femur), intermediate (radio-ulna, tibia), and lower (metapodials) limbs were assessed separately, and were further subdivided into proximal, midshaft, and distal bone sections. My results are consistent with those of Domínguez-Rodrigo, showing that when flesh scraps are present, they typically occur at the joints (proximal and distal ends). Intermediate limb bones preserve flesh scraps more frequently than upper. This finding also lends support Domínguez-Rodrigo's "hot zone" approach to assessing cut mark distribution in archaeofaunal assemblages, which is based on identifying cut marks on areas of bone where flesh scraps no longer remain after lion consumption (see Chapter 3). Metapodials are not high flesh-bearing elements, and so are not included in this analysis. However, in almost every case, when metapodials were preserved, they were unmodified and were still encased in skin.

DISCUSSION

A GIS-Identified Tooth Marking Pattern for Modern Large Felids

Various lines of evidence including bone preservation, the GIS cluster analysis of tooth marking, and gross bone damage patterns in the CTR experimental assemblage all point toward a pattern that large felids cause some degree of bone destruction through gnawing on epiphyses. The degree of destruction is less than what is seen in large canids (wolves) (see Chapter 1), and significantly less than what is seen in spotted hyenas (see Chapter 3). Large felids do not generally fragment long bone shafts, but instead gnaw on and sometimes destroy low density epiphyseal portions, leaving complete bone cylinders with one or both ends missing. Felids may tooth mark long bone shafts, but not nearly as intensively as spotted hyenas do. Significantly dense clusters of tooth marks were identified on all limb elements, and these clusters are mainly on limb bone ends. The frequency of tooth marking imparted by large felids in this study is lower than that produced by hyaenids, while wolf tooth mark frequencies fall between the two. The degree of bone damage produced by these different taxa appears to fall along a continuum with (felids imparting less damage, wolves as intermediate, and spotted hyenas imparting the greatest damage). Because of this, attempts to diagnose signatures of particular carnivore taxa in archaeofaunal assemblages should examine tooth mark frequencies in conjunction with patterns of gross bone damage.

Early Pleistocene Large Carnivores

It is important to acknowledge that while we try to build experimental models that reflect carnivore carcass modification abilities as accurately as possible, there were some important differences in the Early Pleistocene carnivore guild in East Africa, and it is likely that extinct carnivores were involved in modifying archaeological bone assemblages in the past. The

African large carnivore guild during the Plio-Pleistocene included a much larger diversity of taxa than the modern guild. An overview of these taxa is given below, but the focus here is on felid species.

Hyaenids

The extant striped hyena (*Hyaena hyaena*) was present in East Africa during the Early Pleistocene. The dental morphology of *Hyaena* is adapted for bone crunching, which allows it to fill a scavenging niche in modern open-habitat ecosystems (Blumenschine 1987). *Crocuta ultra* is also common in the Plio-Pleistocene of East Africa, and is likely ancestral to the modern spotted hyena (*Crocuta crocuta*) (Lewis and Werdelin 2000). This was a large, robust hyenid, but its tooth morphology suggests it probably did not have the bone crunching capabilities that modern *Crocuta* has (Lewis and Werdelin 2000). The robust *Pachycrocuta*, which is little known in East Africa, and does not persist after the late Pliocene, has been suggested to be a group-living species that may have been somewhat behaviorally similar to *C. crocuta* though less cursorial (Turner and Antón 1995).

An additional now-extinct hyaenid genus found in the African Plio-Pleistocene is *Chasmaporthetes*, often called the “hunting hyena” (Turner 1990). *Chasmaporthetes* had longer limbs and was more lightly built than modern spotted hyenas; it was probably more similar to cheetahs in its cursorial locomotor behavior than to modern hyenas. Tooth morphology of *Chasmaporthetes* indicates hypercarnivory (Hartstone-Rose and Wahl 2008), and it is likely that this taxon was more of an active predator than a scavenger. Lewis and Werdelin (2007) have tentatively suggested that *Chasmaporthetes* could have filled a large-bodied *Canis*-like niche, including the long distance running seen in modern African hunting dogs.

It has been suggested that while the suite of adaptations that characterize modern *Crocuta* (bone crushing dental adaptations, carcass transport, group hunting, and confrontational scavenging) likely developed in this species within the last million years, the multiple species of East African hyaenids in the past probably encompassed these behaviors as a group, and so would have had the same effect ecologically (Lewis and Werdelin 2007).

Canids

The fossil record of canids is more sparse than that of the hyaenids or felids, but at least one now-extinct species of large canid was present in East Africa in the early Pleistocene: *Xenocyon lycanoides* (= *Canis africanus*), and perhaps another species (*Lycaon sekowei*) (Hartsone-Rose et al. 2010), which is newly described and currently known only from South Africa. See Chapter 1 for a full discussion of the large canid fossil record.

Felids

The higher species diversity in the Early Pleistocene carnivore guild compared to the modern African guild is accounted for mainly by felids (Lewis 1997). In addition to modern lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), which are all in the subfamily Felinae, three sabertooth felid taxa (*Homotherium, Dinofelis,* and *Megantereon*), in the now extinct subfamily Machairodontinae were sympatric with early *Homo* before 1.5 Ma (Werdelin and Lewis 2005).

Machairodont felids are characterized by scimitar-shaped upper canines as opposed to the conical upper canine shape seen in modern felids (Biknevicius et al. 1996). Characteristics of the machairodont felids suggest they specialized on large prey; like extant felids they appear to have been flesh-specialists, lacking adaptations for bone crunching (Emerson and Radinsky

1980; Marean 1989). Some have suggested they may have even avoided contact of their teeth with bone in order to protect their canines from breaking (Van Valkenburgh et al. 1990). However, Marean and Ehrhardt (1995) have documented the occurrence of tooth marking on prey animal bones in a *Homotherium* den assemblage, demonstrating that sabertooth felids were capable of imparting tooth marks on bone.

Sabertooth adaptive patterns and behaviors have been reconstructed in some detail. Studies of postcranial ecomorphology (Lewis 1997) as well as stable carbon isotope studies (Lee-Thorpe et al. 2000) indicate habitat differences in these felids. According to these studies, *Dinofelis* and *Megantereon* were probably mixed or closed habitat ambush predators, while *Homotherium* was probably a more cursorial, open habitat species, and possibly a pack hunter (Lewis 1997). Based on ecomorphological analyses of postcrania, Lewis (1997) has argued that sabertooth felids were more behaviorally diverse than modern felids, differing in aspects of habitat use, prey preferences, and perhaps other aspects of their ecology. Because of these differences, Lewis argues sabertooth taxa should be considered individually in their relationship to and effect on hominin behavior. A summary of morphological adaptations attributed to these extinct taxa is provided below.

Dinofelis

Dinofelis is often referred to as the “false sabertooth” because it lacks the highly derived flattened canines of the other machairodonts (Turner and Antón 2004). It has the smallest canines of the sabertooth cats. Its dental morphology falls somewhat between the machairodonts and felines, and for this reason some have included it within the Felinae (Hendey 1974). *Dinofelis* was slightly larger in size than modern leopards, and the enlarged claw on its first digit indicates a difference in the use of its forepaw from modern felids (Werdelin and Lewis 2001).

It also had extremely shortened distal limbs compared to extant felids, suggesting it was not a fast runner and probably inhabited more closed environments. Werdelin and Lewis (2001) argue this morphology indicates *Dinofelis* was probably an ambush predator.

Megantereon

Megantereon had canines that were extremely elongated but much less flattened than the other machairodonts. Its canines were either smooth or possessed slight serrations (Ewer 1973). *Megantereon* was a leopard-sized felid with powerfully developed forelimbs and claws the size of a modern lion. Lewis (1997) has suggested that it was probably an ambush predator or solitary hunter, and that its body proportions indicate it was able to bring down and hold large prey.

Homotherium

Homotherium was the largest of the machairodonts and rivaled modern male lions in size (Turner and Antón 2004). Its distally elongated limbs indicate a cursorial adaptation. Its forelimb morphology also indicates less rotational ability, which suggests it may have had reduced prey grappling abilities compared to modern felids. This implies a fundamentally different means of capturing prey than modern felids (Lewis 1997). Despite its reduced prey grappling abilities, there is evidence that *Homotherium* specialized on large prey. This comes from the Pleistocene site of Friesenhahn Cave in Texas, a den site attributed to *Homotherium* which is filled with tooth marked juvenile mammoth remains. Although juvenile, the mammoth are actually quite large in size (the size of an adult buffalo) (Marean and Ehrhardt 1995). Marean and Ehrhardt (1995) have argued that if *Homotherium* specialized on large prey in North America, it also likely specialized on prey of similar size in Africa. Lewis (1997) has suggested this apparent specialization on large prey, but limited ability of individuals to bring down prey, indicates *Homotherium* may have been a pack hunter. If this is the case, confrontational scavenging from this species by hominins would have likely been difficult, and carcasses left behind by *Homotherium* would have probably provided little scavengable meat.

Overall, characteristics of the machairodont felids suggest they specialized on large prey, and like the extant felines, they were likely flesh-specialists and appear to lack adaptations for bone crunching (Marean 1989). The Plio-Pleistocene felid record is dominated by these sabertooth cats, indicating they were likely a major component of the carnivore guild during this period (Turner and Antón 2004).

The Sabertooth Dentition

One problem with attempts to interpret behaviors of extinct carnivores using experimental models based on modern taxa is that modern carnivores may not provide direct behavioral analogs. This is an issue that has been identified by Domínguez-Rodrigo (2012), although it is not always applied in experimental studies. Several important differences in the masticatory anatomy of sabertooth felids are discussed below.

Incisors

One major part of sabertooth dental anatomy that suggests significantly different carcass processing abilities from modern felids are procumbant anterior teeth (incisors and lower canines). In most carnivores (including canids and hyaenids), the incisors are arranged in a procumbant, semicircular arc that functions as a “grasping” region of the dentition and is used for biting during hunting and stabilizing prey while killing (Biknevicius and Van Valkenburgh 1996). The small, conical incisors of extant felids are not arranged in this fashion, but instead are anchored upright in the jaw. Because of this, the incisors of extant felids have a reduced grasping ability. They instead functionally serve to buttress the canines, which are used for killing bites (Biknevicius et al. 1996). In modern felids, the carnassial region is then used to deflesh prey (Biknevicius et al. 1996; Biknevicius and Van Valkenburgh 1996; Van Valkenburgh 1996). The functional suite of the anterior dentition in sabertooth felids is actually more similar to canids or hyaenids than to modern felids (Biknevicius and Van Valkenburgh 1996). Sabertooths may have relied more strongly on their incisors than living felids do, and may have used them for prey stabilization during killing and feeding (Biknevicius and Van Valkenburgh 1996). They very likely defleshed carcasses in a way more similar to canids with their anterior dentition (Hartstone-Rose 2008).

Canines

The most obvious dental difference between extinct machairodont felids and modern felids is their long and laterally compressed sabertooth canine. Due to their long, thin shape, sabertooth canines were probably more prone to breakage than the shorter, more robust canines of modern felids. It has been suggested that in order to protect the canine from breakage, they may have avoided contact with bone (Emerson and Radinsky 1980; Van Valkenburgh and Ruff, 1987; Marean 1989). In fact, high frequencies of canine breakage have been identified in Pleistocene sabertooth species from North America (Van Valkenburgh and Hertel 1993). The canines of *Dinofelis* were shorter and broader than the other Machairodonts, and so were probably somewhat more stress resistant (Marean 1989).

In almost all carnivores, canines are used to deliver killing bites. These bites may be shallow and slashing (as in canids), or deep and penetrating (as in modern felids) (Marean 1989). Because a deep bite would risk breaking the tooth, sabertooth canines were more likely used in a slashing manner on convex body surfaces to create large superficial wounds (Emerson and Radinsky 1980). Also, the ability of sabertooths to open the jaws widely would have been critical for use of the canines. From a functional analysis of gape, Emerson and Radinsky (1980) showed that sabertooths did not have any more clearance between the upper and lower canines than modern felids do, further suggesting that sabertooth canines were used to make superficial rather than deep wounds. Because of their ability to make larger killing slashes with the canines, sabertooth felids may have been able to take down larger prey sizes (medium to large sized ungulates) than modern felids can (Emerson and Radinsky 1980).

Postcanine Dentition

The postcanine region is arguably the most important part of the dentition in terms of determining a carnivore's carcass processing abilities (Hartstone-Rose 2008). This region consists of the premolars and the carnassial complex. The carnassial region is a defining feature of all carnivores, and is a highly specialized functional complex used for slicing flesh (Marean 1989; Van Valkenburgh 1989). Anterior to the carnassial, the premolars are modified in different ways to accommodate processing of different diets. Hyaenids, for example, use their premolars to crush bone, whereas felids use them to slice flesh (Hartstone-Rose 2008). The premolars of sabertooth felids are reduced in size and sometime in number, suggesting that this region was not as important to carcass processing as in modern felids, or possibly because it was interfering with the large maxillary canine (Hartstone-Rose 2008).

Felids can crush bone to some degree, but this is normally done with the premolars as the molar region - which is used for grinding and bone crushing in other carnivores - is greatly reduced in felids (Marean 1989). Because leverage is reduced further forward in the mouth, it has long been suggested that bite force in sabertooth felids may have been weaker than in modern felids (Matthew 1910). However, recent studies have suggested that estimating bite force is more complex than previously assumed and involves other factors such as muscle fiber orientation in relation to gape angle (Slater and Van Valkenburgh 2009; Christiansen 2011; Hartstone-Rose et al. 2012). Musculature can thus be modified in ways to maximize bite force. Given this, it is currently unclear whether sabertooth felids had lower bite force than modern large felids.

Dietary Reconstruction for Sabertooth Felids Based on Postcanine Dental Morphology

Sabertooth felids were almost certainly hypercarnivorous. However, in an attempt to further characterize the diet of these extinct felids, Hartstone-Rose and Wahl (2008) conducted a study based on aspects of the postcanine dentition. They found that the radius of curvature on postcanine teeth (a measurement of occlusal bluntness) is tightly correlated with feeding behavior in modern carnivores and accurately separates durophage specialists (which have relatively blunt teeth) from meat specialists (which have sharper teeth). They applied this measure to fossil felids in order to deduce carcass processing abilities, and found that sabertooth felids (particularly *Dinofelis* and *Homotherium*) do not appear to have been more hypercarnivorous than modern felids. Other measures of carnivore tooth morphology that correlate with dietary category also confirm that extinct felids were within the same dietary range as modern felids with respect to flesh specialization (Hartstone-Rose 2011).

Tooth Marking Abilities of Sabertooth Felids

The premolars and carnassials of sabertooth felids are largely similar to those of extant large felids. As it is the postcanine dentition that is responsible for defleshing, Domínguez-Rodrigo (2007a) has argued that these dental similarities indicate defleshing behaviors and abilities of sabertooth felids may have been the same as those documented in modern felids.

However, given the elongated canine, it is difficult to envision sabertooth felids manipulating bones in their mouths in exactly the way that modern felids do. Sabertooth felids almost certainly did some defleshing with their incisors in the same way that canids do. They also likely defleshed bones with their premolars by carefully sliding bones into the side of the mouth to produce slicing bites as modern felids sometimes do (Hartstone-Rose 2008). There is currently no firm evidence that extinct felids were less capable of imparting tooth marks on bone than extant large felids. In fact, evidence from the Friesenhahn Cave site in Texas (a den site attributed to *Homotherium*) shows sabertooths were capable of tooth marking bones, though they do not often crack them (Marean and Ehrhardt 1995).

CONCLUSIONS

This discussion has shown that although modes of prey capture may have differed in sabertooth felids, as suggested by their differing postcranial and anterior tooth morphologies, similarity in postcanine dentition indicates bone damage patterns imparted by extinct felids are likely to have been similar to those produced by modern felids. If anything, sabertooth felids could have been capable of producing slightly greater bone damage than modern large felids. With these considerations in mind, is reasonable to use modern large felids as analogs for interpreting bone damage potentially inflicted by large felids in the past.

The pattern observed in the study presented here shows that the largest extant felids produce less bone damage than large canids or spotted hyenas. Felids in the CTR study tooth marked limb bone midshafts of size 2 carcasses at a frequency of approximately 11%, whereas canids tooth mark midshafts of similarly sized bones at frequencies between 12-32% (see Chapter 1). Hyenas have been reported to tooth mark midshafts much more frequently up to 70% for small carcasses

(Blumenschine 1995; Faith 2007). For larger carcasses, CTR felids tooth marked limb bone shafts 58% of the time, more frequently than I found in my wolf samples (23-40%) (see Chapter 1), but still less frequent than has been reported for spotted hyenas by Blumenschine (88%) or Faith (75%). The small sample size for large carcasses in the CTR study may account for the higher than expected tooth mark frequency imparted by felids on large carcasses in this study.

Overall patterns of bone damage from this study show that felids leave relatively complete bones after feeding, which show a majority of tooth marking on the ends, leaving limb bone shafts relatively free of marking. Large felids can and sometimes do gnaw on limb bone ends destroying the epiphyses to some degree in size 2 carcasses, but limb bones are rarely fragmented to the degree that hyaenids or even canids are capable of. Bone portion survivorship and tooth mark clustering patterns are best viewed as a continuum in which large felids process bone less thoroughly than hyaenids, and large canids are intermediate in their processing abilities. This illustrates the importance of examining multiple lines of evidence including gross bone damage patterns in addition to tooth mark frequencies in interpreting carnivore carcass processing activities in the past (Pobiner 2007).

Results from the study of flesh availability in the CTR experiments show that large felids typically deflesh upper and intermediate limb elements of size 2 carcasses. Bulk flesh is rarely preserved. When flesh scraps are preserved, they occur more frequently on the intermediate rather than upper limb elements. This finding is consistent with Domínguez-Rodrigo and colleagues' (2007a) similar study of flesh availability on larger-sized carcasses, and suggests that passive scavenging by hominins in the past would not likely have yielded significant quantities of flesh.

CHAPTER 3. A GIS Image Analysis Approach to Oldowan Hominin Meat Eating at Kanjera South, Kenya

ABSTRACT

This study examines the timing of hominin and carnivore access to carcasses in the ca. 2 Ma zooarchaeological assemblage from Kanjera South through an analysis of hominin- and carnivore-induced bone modification patterns. I argue that the Kanjera assemblage offers some of the earliest clear evidence of routine butchery of large mammal carcasses by early members of the genus *Homo*, in concordance with the findings of initial studies of the Kanjera fauna (Ferraro 2007; Ferraro et al. 2013). I used GIS to record bone preservation in the Kanjera assemblage as well as in several modern, experimentally-modified bone assemblages, which are used for comparison. I documented the placement of hominin- and carnivore-induced modifications on bones from these assemblages, and using the GIS Spatial Analyst, identified where particular types of modifications clustered. Results show that the pattern of bone preservation at Kanjera is similar to GIS-generated models based on experimental bone assemblages that were first butchered and hammerstone fractured by humans, and subsequently scavenged by carnivores. The distribution of bone modifications on the Kanjera fauna also suggests hominins had early access to small bovids. Butchery marks appear almost exclusively in “hot zones” (Domínguez-Rodrigo et al. 2007) – areas where flesh never survives lion consumption – further suggesting hominins at Kanjera were not scavenging carnivore kills. Overall frequencies of both hominin and carnivore modifications are lower than those at the slightly younger site of FLK Zinj (Olduvai Gorge, Tanzania), suggesting differing competitive regimes at the two sites.

INTRODUCTION

Understanding the diet and subsistence behaviors of the earliest members of the genus *Homo* is central to understanding the behavioral ecology of early hominins and to understanding the ecological context of human evolution on a broader scale. As a high-quality resource that provides protein, fat, and many micronutrients, the importance of animal tissue in the diet and its method of acquisition are of particular interest. We know that as hominin brain size and energy demands increased, meat was incorporated into the diet (Aiello and Wheeler 1995), but we do not know how meat was acquired or to what degree hominins competed with carnivores over this resource. Current hypotheses argue for various modes of carcass acquisition by hominins including hunting (Domínguez-Rodrigo and Pickering 2003; Domínguez-Rodrigo and Barba 2006), active scavenging, where hominins drove carnivores away from fresh kills (Bunn and Ezzo 1993), or passive scavenging, where hominins acquired carcass parts late in the consumption sequence of a carcass (Blumenschine 1988,1995). Patterns of hominin-induced butchery marks and carnivore gnawing marks on fossil mammalian remains provide insight into these activities. However, our current understanding is limited by 1) being mainly confined to studies of a single archaeological site (FLK Zinj, Olduvai Gorge, Tanzania) and 2) lack of a firm methodology to quantify bone preservation and surface modification patterns.

This study will address the issues above by applying a new geographic information systems (GIS)-based method to an analysis of bone modification patterns in the archaeofaunal assemblage from Kanjera South, Kenya, a site slightly older than the occurrences in Bed I, Olduvai Gorge. I will also use modern carnivore-gnawed assemblages created under controlled conditions as a baseline for comparison with and interpretation of the Kanjera assemblage. Because Kanjera South is close in age to the Bed I Olduvai sites, but deposited in a different environmental context, the site provides an ideal opportunity to explore potential variability in hominin and carnivore interactions during the Oldowan. This will be further explored in Chapter 4.

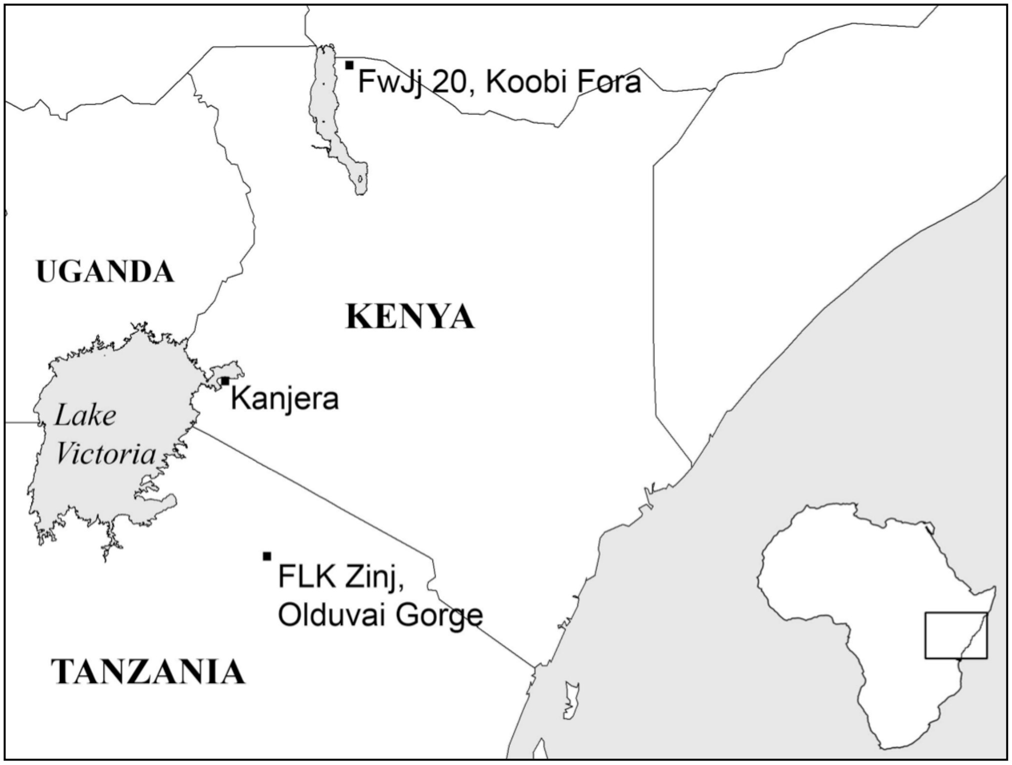
BACKGROUND: KANJERA SOUTH (KENYA)

Kanjera South - Site Context

Setting

The approximately 2 Ma site of Kanjera South (KJS) is located on the Homa Peninsula of Lake Victoria in Western Kenya (Fig. 3.1). Three excavations at KJS covering an area of more than 169m^2 have yielded *in situ* Oldowan archaeological materials in the three lowermost beds at the site (KS-1 through KS-3) in a sequence approximately 3m thick (Plummer et al. 1999; Bishop et al. 2006; Ferraro 2007; Plummer et al. 2009a; Ferraro et al. 2013). The context of each bed is described in detail by Ditchfield et al. (1999). More than 2900 Oldowan artifacts and over 3500 identifiable fossils, including butchery-marked bones have been recovered from the site. Taphonomic and zooarchaeological analyses indicate the site formed predominantly through hominin agency (Ferraro 2007; Plummer 2009b; Ferraro et al. 2013).

Figure 3.1. Location of Kanjera South in relation to some other Oldowan sites.



Historical Context

The earliest investigations at Kanjera were conducted by Oswald (1914) and recovered the first monkey fossils discovered in East Africa. Work was continued on the Homa Peninsula by Leakey (1935), who discovered cranial remains of at least three anatomically modern humans at Kanjera and the nearby site of Kanam. Leakey claimed that the apparent association of these remains with Middle Pleistocene fauna provided evidence for the great antiquity of *Homo sapiens*. However, Leakey's interpretation was controversial because he did not record the precise location of the finds, most of which were surface collected. An expedition by the Smithsonian Institution in 1987-88 recovered additional hominin fossils. Plummer and colleagues have since reexamined the sample and have determined the hominins postdate deposition of the Kanjera Formation and likely represent intrusive Holocene burials into the ancient sediments (Plummer et al. 1994; Plummer and Potts 1995).

The geology and paleontology of the Homa Peninsula were subsequently described in further detail by Kent (1942), Pilbeam (1974), and Pickford (1984). The Homa Peninsula Paleoanthropological Project began further investigation of the area in 1987 (Plummer and Potts 1989; Plummer 1992; Ditchfield et al. 1999; Plummer et al. 1999), and has been conducting excavations at Kanjera South since 1995 which have recovered abundant, *in situ* Oldowan artifacts and fauna. The bulk of the faunal sample was recovered between 1995 and 2001. Additional specimens were recovered from excavations in 2009 in Beds KS-1 and KS-2 and are reported on for the first time here.

Kanjera South Depositional Environment

Deposition of the Kanjera Formation is consistent with a lake margin setting. With the exception of a few diffuse conglomerates, the KS-1 through KS-3 sequence is composed of sands and sandy silts deposited by ephemerally flowing, low aspect channels, which were flowing northwards toward what was probably an ancient lake. Intermittent paleosol formation in multiple horizons indicates stable land surfaces formed at times (Ditchfield et al. 1999; Plummer 1999; Plummer et al. 2009b). A somewhat wetter depositional environment is indicated in KS-3 by an increase in hippopotamid representation in the assemblage, evidence for soft sediment deformation, and the preservation of a small channel. This wetter trend continues into Bed KS-4 with the transgression of the lake capping the archaeological sequence (Plummer et al. 2009b). Sedimentary analyses reveal that lithics and fauna are out-sized clasts relative to grain size, indicating water-flow is not responsible for site formation. There is also a mixture of skeletal parts with differing hydraulic transport potentials, and several artifact and fossil refits have been made, further suggesting a primary context for the site (Plummer et al. 1999; 2009a). Estimated rates of sedimentation and pedogenesis suggest the fauna and artifacts accumulated relatively rapidly over a period of decades to centuries (Plummer et al. 2009b; Ferraro et al. 2013). There is little evidence of weathering or sedimentary abrasion on the fauna, which also indicates that the site was buried quickly. Further, the overall abundance and taxonomic diversity of faunal remains exceed what is expected in natural landscape accumulations (Ferraro et al. 2013). This combined evidence of the deposition of sediments and fauna at Kanjera South indicates primary context for fossils and artifacts at the site and rapid burial, making Kanjera South an ideal candidate site for addressing questions about early hominin foraging ecology.

Locality Age

Finds at Kanjera are well dated to ca. 2 Ma based on paleomagnetic and biostratigraphic analyses. The co-occurrence of both the proboscidean *Deinotherium* sp. and the suid *Metridiochoerus andrewsi* (last appearance datum for both is ca. 1.7 Ma) with *Equus* (first appearance datum in East Africa is ca. 2.3 Ma) bracket the Kanjera sediments within this period (Harris 1978; Harris and White 1979; Werdelin and Sanders 2010). The presence of a normal zone of geomagnetic polarity identified as the Olduvai Subchron (1.77-1.95 Ma) in the upper part of the sequence further constrains the archaeological levels to 2.3-1.95 Ma (Ditchfield et al. 1999; Plummer et al. 1999).

Paleoenvironmental Context

The paleoenvironmental context at Kanjera is unique in that it provides the earliest evidence for hominin activities within a grassland-dominated ecosystem. In contrast, most other Oldowan occurrences have been reconstructed as woodland settings (Cerling and Hay 1986; Sikes 1994; Ashley et al. 2010). Taxonomic representation and isotopic analyses indicate Kanjera was deposited in a relatively open (C_4 grass-dominated) context (Plummer et al. 2009b). The majority of the faunal sample at Kanjera consists of grassland-adapted bovids (*Parmularius, Antidorcas*). Equids (*Equus*, *Eurygnathohippus*) and suids (*Metridiochoerus*), along with some water-dependent taxa (e.g., *Hippopotamus*, *Crocodylus*, and reduncine bovids) are present but less common (Plummer et al. 2009a,b). Isotopic analysis of dental enamel indicates these taxa had a large amount of grass in their diets. This is even the case for taxa that normally have a C_3-rich (fruit or browse) diet (e.g., *Cercopithecus* sp. and *Deinotherium* sp.) (see Cerling et al. 1999; Sponheimer and Lee-Thorp 1999). Isotopic analyses of pedogenic carbonates also indicate a grassland setting.

Lithic Technology

Use-wear analysis of stone tools from Kanjera suggests tools were used for a variety of tasks including butchery, wood-working, processing of underground storage organs, and cutting of grass or reeds (Lemorini et al. 2009; Lemorini et al. in review). Raw material source analysis of the lithic assemblage indicates stone material was habitually transported over longer distances than has previously been documented in the Oldowan, with higher quality raw material (harder, more easily flaked material) being preferentially transported and more carefully flaked (Braun et al. 2008, 2009). Research on the lithics to date indicates that hominins at Kanjera had a good understanding of the physical properties of different raw materials and made selective transport decisions based on this understanding. The aim of this project is to further investigate this type of behavioral variability in Oldowan hominin meat acquisition activities through a comparative analysis of the Kanjera taphonomy with that at another Oldowan site: FLK Zinj.

Kanjera South Zooarchaeology Overview

Bovid remains dominate the KJS assemblage (followed by equids and suids), and represent a minimum of 56 individuals (Ferraro et al. 2013), making this one of the larger faunal assemblages of Oldowan age. The majority of bovid individuals are small (Bunn's size class 1 and 2) or medium (Bunn's size class 3) in size, and many of these (about 50%) are subadult (Bunn 1982; Ferraro 2007). The most common bovid species at KJS are the extinct alcelaphine *Parmularius altidens* and the antilopine *Antidorcas recki*. Larger bovids (size 3b and above) are not well represented, and so the discussion here will mainly focus on the small and medium-sized individuals.

From his analysis of the Kanjera fauna, Ferraro (2007) argued that hominins had early access to small (size 1 and 2) bovids at the site, possibly obtained through hunting. His argument is partially based on hominin damage to bones, including the anatomical placement of cutmarks, which occur on meaty limb elements. However, there is also evidence of carnivore activity at the site (Fig. 3.2).

Carnivore Tooth Mark Frequencies

It is well known that the frequency and location of carnivore tooth marks on skeletal remains can provide important information regarding the timing of access to carcasses by

Figure 3.2. Examples of bone surface modifications found in the KJS assemblage.
a. cut marked rib (#24434), b. femur with percussion notch, view from medullary surface (#5268), c. percussion marks on long bone shaft fragment (#24844 from 2009 excavation), d. carnivore tooth score on head of femur (#2565), e. carnivore tooth pit on rib (#15054).

Photos a-c and e courtesy of James Oliver carnivores. Experimental work has shown that tooth mark frequencies vary in a predictable way based on whether carnivores have earlier or later access to carcasses (Blumenschine 1988, 1995; Selvaggio 1994a, 1998; Capaldo 1998b; Lupo and O'Connell 2002; Domínguez-Rodrigo and Pickering 2003). When carnivores have early access to fully fleshed carcasses or limbs, they typically tooth mark long bone midshafts at high frequencies (>75% of NISP). However, if limbs have been previously defleshed and demarrowed by humans, the frequency of tooth marked midshaft specimens is much lower (5-15% of NISP), as broken shaft fragments have minimal nutritional value (Blumenschine 1995; Capaldo 1998b; Marean et al. 2000). In both early and later access scenarios, the frequency of tooth marking on the epiphyses is equally high (>70% of NISP). This makes the midshaft tooth marking frequencies most informative regarding timing of access. Assessing the frequency of tooth marking in fossil assemblages using these experimental frameworks can aid in interpreting the extent and timing of carnivore involvement in assemblages.

Ferraro et al. (2013) clearly showed tooth mark frequencies at KJS most closely resemble the frequencies from experimental models where humans were the agents of defleshing and butchering and where carnivores had secondary access to defleshed and demarrowed bone refuse. Tooth mark frequencies on midshaft specimens in the total Kanjera assemblage (summed Beds KS-1- KS-3, all size classes) are between 8-14%, with frequencies in each bed falling within or even slightly below the range in hominin-first assemblages. These consistent frequencies across beds reflect a repeated pattern through time of early access by hominins to carcass remains.

Epiphyses exhibit higher frequencies of tooth-marking in both carnivore first and hominin first access scenarios (50-100%). In contrast to these experimental models, the KJS pattern of epiphyseal tooth marking in summed bed assemblages ranges between 12-18% (Ferraro et al. 2013), suggesting low on-site competition at Kanjera. These tooth marking results are similar if broken down by size class or bed.

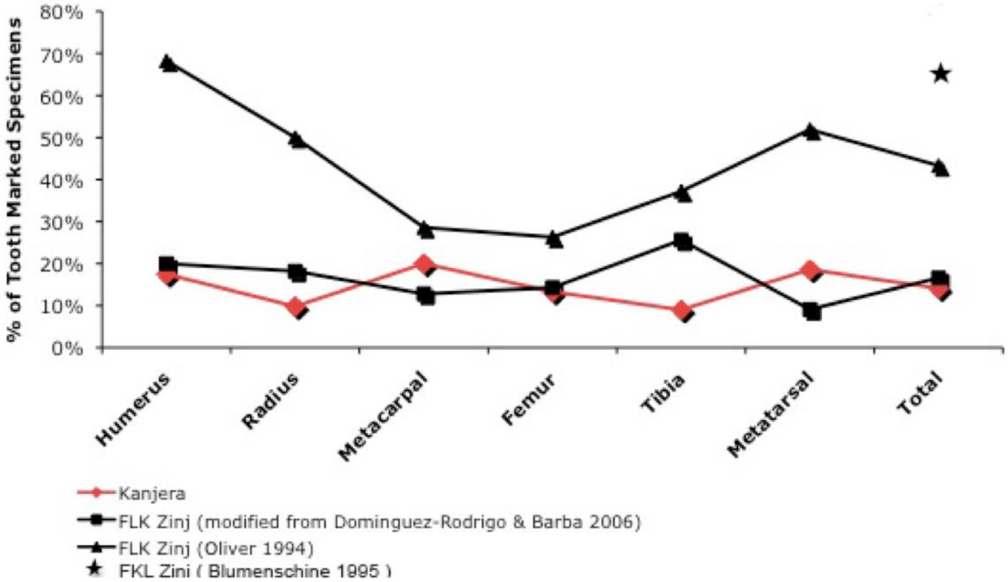
Kanjera Tooth Mark Frequencies Compared to FLK Zinj

Assemblage-wide tooth mark frequencies by skeletal element calculated in this study are shown in Figure 3.3 and Table 3.1 and compared with frequencies reported by other researchers for FLK Zinj. Compared to FLK Zinj, the Kanjera tooth marking frequencies are low (approximately 14% as calculated in this study). Frequencies reported for FLK Zinj by Oliver (1994) for small bovids are approximately 43%. Blumenschine's (1995) frequency is somewhat higher (65%). Domínguez-Rodrigo's group has reported much lower frequencies (close to what I found for Kanjera) at FLK Zinj. This discrepancy in reports is troubling. The problem lies partly in the different criteria that are used to identify tooth marks, but this issue also highlights the potential of the GIS image analysis method to help interpret sites in a more meaningful way by examining patterns of tooth marking in addition to frequencies. This issue as it relates to FLK Zinj will be examined further in Chapter 4.

Cut Mark Frequencies

Ferraro et al. (2013) reported cut mark frequencies on limb bone specimens in the total KJS assemblage (Beds KS-1 through KS-3 summed) between 1.9%-6.3%. They argue that because these frequencies are uniform throughout the assemblage (they are consistent regardless of analyst, bed, or animal body size), this reflects a consistent pattern of carcass exploitation practiced by hominins at KJS. These frequencies are lower than the frequency produced in some modern, experimentally produced and ethnoarchaeological assemblages (e.g., Domínguez-

Figure 3.3. Percent of small and medium-sized tooth marked specimens from Kanjera compared with FLK Zinj



Kanjera data includes Beds KS-1 through KS-3 combined and includes size classes 1-3a. Data from Table 3.1. Only Blumenschine's total is plotted, as his data are not reported by anatomical part.

Table 3.1. Tooth marked specimens from Kanjera by limb for small and medium-sized bovids compared with FLK Zinj

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal	Total
Kanjera South (this study)	11/63 (17.5)	5/51 (9.8)	7/35 (20)	6/45 (13.3)	5/56 (9)	5/27 (18.6)	39/277 (14.1)
FLK Zinj (Oliver 1994)	15/22 (68.2)	9/18 (50)	6/21 (28.6)	5/19 (26.3)	16/43 (37.2)	14/27 (51.9)	65/150 (43.3)
FLK Zinj (modified from Domínguez-Rodrigo and Barba 2006)	7/35 (20)	4/22 (18.2)	4/34 (12.8)	3/21 (14.3)	11/43 (25.6)	4/44 (9.1)	33/199 (16.6)

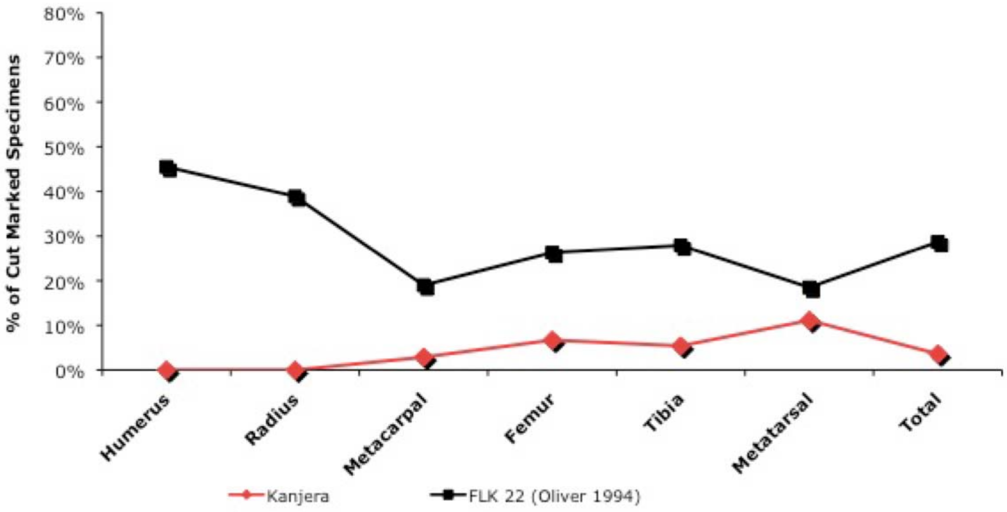
The top number represents the number of tooth marked specimens / total number of identifiable specimens for that element. The number in parentheses represents percentage of tooth marked specimens. Kanjera specimens represent only those identifiable to element, and also include material from 2009 excavations. Specimens from Kanjera include sizes 1-3a, as a majority of elements are on the boundary between size 2 and 3a. Data reported by Oliver (1994, Table 1) are for size 1 and 2. Data from Domínguez-Rodrigo and Barba (2006) for size 1 and 2 carcasses are modified from their Table 3. Their data were presented by bone section (shafts and ends), not by complete bone. Tooth marks include tooth pits, punctures, and scores.

Rodrigo 1997; Lupo and O’Connell 2002). However, similarly low frequencies of hominin cutmark and percussion damage have been found in other Early Stone Age assemblages (e.g., Monahan 1996; Egeland et al. 2008; Pobiner et al. 2008; Domínguez-Rodrigo et al. 2009; McCoy, 2009) and some Middle Paleolithic and Late Stone Age assemblages to which hominins certainly had primary access (e.g., Guilday et al. 1962; Cruz-Uribe and Klein 1994; Stiner 2005; Dewar et al. 2006).

Cut mark frequencies for just the small and medium bovids at KJS varies between 2.0–5.9% depending on observer (Ferraro et al. 2013, Table S1). Bone surface damage was assessed in Ferraro’s (2007) study independently by 3 observers, and my independently calculated frequencies are within this range at 3.6% (Table 3.2). Only bones with good cortical surface preservation are considered here (as well as in Ferraro’s study) to reduce any bias that might appear due to differing preservation between the KJS and FLK Zinj assemblages. The occurrence of cut marks on meaty limb elements indicates early access at Kanjera. However, cut mark frequency counts are much lower than what is seen at FLK Zinj (Fig. 3.4), suggesting hominins had early access to carcasses at Kanjera, but were not processing them as completely as at Olduvai.

Cut marks on rib elements also indicate flesh removal by hominins (Fig. 3.5). Ferraro et al. (2013) report cut mark frequencies on the ribs in KS-2 range from 9.7%-12.9% for small animals, and 5.0%-7.5% for medium-sized animals, which they argue clearly indicates hominin removal of soft tissue. Further, ribs are not high survival elements, and based on experimental models are not predicted to survive carnivore consumption. The presence of a relatively high frequency of cut marked ribs at KJS reflects early and perhaps exclusive hominin access to some carcasses.

Figure 3.4. Percent of small and medium-sized cut marked specimens from Kanjera compared with FLK Zinj



Kanjera data includes Beds KS-1 through KS-3 combined and includes size classes 1-3a. Data from Table 3.2.

Table 3.2. Cut marked specimens at Kanjera by limb for small and medium-sized bovids compared with FLK Zinj

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal	Total
Kanjera South	0/63 (0)	0/51 (0)	1/35 (2.9)	3/45 (6.7)	3/56 (5.4)	3/27 (11.1)	10/277 (3.6)
FLK Zinj (Oliver 1994)	10/22 (45.5)	7/18 (38.9)	4/21 (19)	5/19 (26.3)	12/43 (27.9)	5/27 (18.5)	4/150 (28.7)

The first number represents the number of cut marked specimens / total number of identifiable specimens for that element. The number in parentheses represents percentage of cut marked specimens. Kanjera specimens represent only those identifiable to element, and also include material from 2009 excavations. Specimens from Kanjera include sizes 1-3a, as a majority of elements are on the boundary between size 2 and 3a. Data reported by Oliver (1994, Table 1) are for size 1 and 2.

Percussion Marks

Hammerstone-induced percussion marks indicating marrow extraction provide further evidence for hominin involvement with carcasses. Percussion marks at KJS show clear hallmarks of hominin-induced percussion breakage including pits and striae (Blumenschine and Selvaggio 1988). The frequency of percussion marking on midshafts in the KJS assemblage ranges from 6-9% (Ferraro et al. 2013). In both KS-1 and KS-2, frequencies of percussion

Figure 3.5. Cut marks on medial surface of rib (specimen #25200 from 2009 excavation). Scale is in mm.

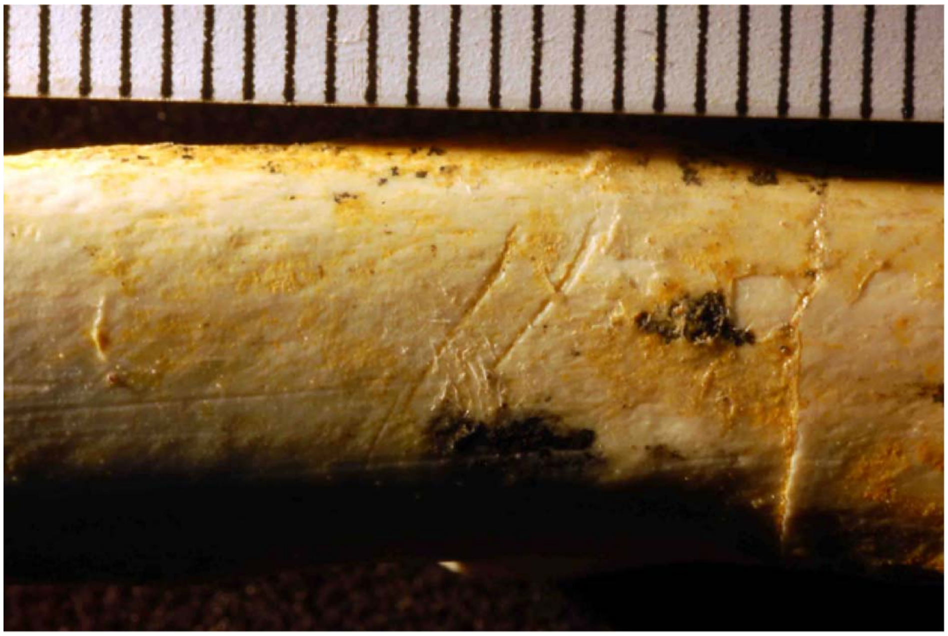


Photo courtesy of James Oliver

marked limb elements also increase with prey size, with larger individuals being more heavily damaged. However, the Kanjera percussion mark frequencies fall well below the 95% confidence intervals of experimentally hammerstone fractured assemblages, which range roughly between 39-49% (e.g., Blumenschine 1995; Capaldo 1995, 1998b; Marean et al. 2000).

While the presence of bone surface modifications associated with butchery and hammerstone percussion clearly indicate hominin exploitation of meat and within-bone tissues, directly extrapolating cut and percussion mark frequency data to estimate intensity of carcass processing can be problematic. Experimental research has failed to show a consistent link between the number of cut and percussion marks and the intensity of processing (Egeland 2003; Lyman 2005; Pickering and Egeland 2006). For example, experimental work by Pickering and Egeland (2006) found no relationship between percussion mark frequency and the number of hammerstone blows. Experiments by Pobiner and Braun (2005) found no relationship between the number of cut marks produced and the amount of meat removed during butchery. A number of variables including degree of assemblage fragmentation, fossil surface preservation, carnivore ravaging, carcass size, and tool type play a role in determining both percussion and cut mark frequency (Domínguez-Rodrigo and Yravedra 2009), making interpretation of frequencies more complex than some earlier models have assumed (e.g., Binford 1981; Bunn and Kroll 1986; Shipman 1986). Lyman (2005) argues that cut marks should be viewed as behavioral "epiphenomena," or byproducts of hominin butchery, which indicate involvement with carcasses, but without a direct relationship to the degree of involvement.

Given the complications with interpreting cut mark frequencies in light of these factors, a combination of frequency data along with other zooarchaeological measures such as the anatomical placement of cut or percussion marks on bones should be used to investigate the timing of access to carcasses by hominins. Domínguez-Rodrigo (1997) has suggested that a combined analysis including overall frequency, differential distribution of cut marks on meat-bearing versus non-meat bearing limb bones, and the presence of cut marks on midshaft sections of meat-bearing limb bones is the most useful approach for distinguishing primary from secondary access by hominins. In my work, I attempt to define additional measures for examining hominin carcass access by using GIS to spatially locate significantly dense clusters of bone surface modifications in experimental samples. These experimental models provide an additional framework for interpreting the behavioral agents involved in assemblage formation.

Element Representation

In terms of bone element representation, there are some interesting differences between the small and medium-sized bovids at KJS. Size 1 and 2 bovids, which are most commonly found in the assemblage, show a relatively even representation of skeletal elements (Shannon's evenness index: 0.924-0.955 in Ferraro et al. 2013), with the whole range of skeletal elements preserved in the assemblage. This suggests small bovids were transported to the site as whole carcasses. The size 3 bovids show a somewhat different pattern. Although all skeletal regions are present, cranial remains dominate the assemblage, and meaty upper limb bones (humerus and femur) are more abundant than lower limb bones or axial elements. Ferraro and colleagues (2013) have argued this pattern does not resemble a typical background scatter or landscape bone assemblage. Instead, they have interpreted it as suggestive of a "weight minimizing strategy," where certain high-yielding carcass parts from medium-sized animals were selectively transported to the site.

Ferraro and colleagues (2013) argue that selectively transporting the heads may be a distinct scavenging strategy. Within-head resources including the brain, tongue, and mandibular marrow are fatty, nutrient-rich sources of food. Further, during times of seasonal resource stress, fat deposits are depleted last in the mandible and brain (Speth 1983, 1990). If hunters are energy-limited, fat is more valuable than the protein in lean meat, which takes more energy to digest. Under circumstances of seasonal stress, a focus on within-head tissues may be an effective dietary strategy. This is a strategy that is documented in modern hunter gatherers as well (Speth 1990).

The hominins at KJS seem to have been practicing different strategies in regard to the small and medium-sized bovids. The evidence thus far indicates small bovids were transported to and deposited at the site as whole carcasses. This must have happened early in the resource life of the carcass, as large African predators such as lions and hyenas tend to completely consume small-sized carcasses, leaving little or no scavenging opportunities behind (Blumenschine 1987). Given the evidence from skeletal part representation and evidence of butchery marks, Ferraro and colleagues have argued that the small bovid remains at KJS may represent the earliest evidence of hunting in the archaeological record. Medium-sized carcasses on the other hand, may reflect a separate, distinct scavenging strategy.

This Study

This study builds on previous taphonomic work at Kanjera by applying a GIS image analysis method to examine bone preservation and modification patterns in the KJS assemblage. These patterns will be assessed relative to GIS models based on experimentally modified assemblages created by humans and various species of large carnivores. By examining specific patterns of bone modification in addition to modification frequencies, taphonomic patterning can be examined on a finer level than has been done thus far, providing new insights into hominin and carnivore activities at the site.

METHODS

Identification of Bone Surface Modifications

Several different types of hominin- and carnivore-induced bone surface modifications are identified and analyzed. I have identified these modifications based on published criteria. Several important terms are defined here.

1. *Carnivore tooth pits* are defined as circular or oval marks on bone resulting from the tooth pressing against the bone surface. *Punctures* result when the bone collapses under the pressure of the tooth (Binford 1981; Haynes 1980; Lyman 1994 and references therein)

2. *Tooth scores* are linear marks (at least three times as long as they are wide) that result from the tooth dragging across the surface of the bone. Scores are U-shaped in cross section, and often perpendicular to the long axis of the bone. Tooth *furrows* are deeper marks that penetrate

through the cortical surface of the bone (Haynes 1980; Binford 1981; Selvaggio, 1994b; Domínguez-Rodrigo and Barba 2006).

3. *Cut marks* are linear marks that are distinguished from carnivore tooth scores by their V-shaped cross section, and by the multiple, fine, parallel striae within the mark (Binford 1981; Bunn 1981; Potts and Shipman 1981; Shipman 1981).

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

5. *Percussion notches* are defined as "semicircular or arcuate indentations on the fracture edge of a long bone" (Capaldo and Blumenschine 1994). These are produced by dynamic loading on the cortical surface of the bone, and display an adjacent negative flake scar on the medullary surface. In this study, percussion notches were distinguished when possible from carnivore tooth notches, and if there was any ambiguity, notches were classified as indeterminate and excluded from the analysis. Percussion notches were distinguished based on their broader shape in cortical view. Tooth notches tend to be more semicircular than hammerstone notches, and have a flake release angle closer to perpendicular compared with the obtuse release angle for hammerstone produced flakes (Capaldo and Blumenschine 1994). Further, percussion notches and tooth notches can also be distinguished by cut marks or tooth marks associated with the notch.

In experimental assemblages where the agent of modification was known, marks were relatively easy to classify, and identifications were based on the presence of classic features defined above. In fossil assemblage, where all potential contributing taphonomic factors are unknown, I first attempted to exclude any types of pseudo-marks (e.g., marks created by trampling, sediment abrasion, or excavation tools) (Behrensmeyer et al. 1986; Domínguez-Rodrigo and Barba 2006). Following Oliver (1994), when mark morphology was ambiguous, I assessed the mark in light of surrounding carnivore- or hominin-induced damage. This is a conservative approach to identifying bone surface modifications, but it reduces error by examining marks as a suite of related damage points. Following Ferraro's (2007) protocol, I excluded fossils with poor surface preservation and recent breaks from my analysis.

GIS Image-Analysis

I used the GIS image analysis method initially described by Marean and colleagues (Marean et al. 2001; Abe et al. 2002) and expanded in Chapter 1 and in Hodgson et al. (2010) to plot bone fragment shapes onto template graphics in GIS. In order to assure bones were placed accurately on the template, analysis was restricted to fragments that were identifiable to element and side. Using GIS, bone surface modifications were also plotted onto the digital image of each fragment in order to create composite images of bone modification distributions for each element.

Hot Zone Approach

In addition to GIS analyses, I apply a “hot zone” approach (following Domínguez-Rodrigo et al. 2007) to assess whether hominins were accessing fleshed carcasses prior to large felids. Domínguez-Rodrigo conducted a study documenting kills made by lions in the wild and observed that lions do not always consume all the flesh on bones (Domínguez-Rodrigo 1999; Domínguez-Rodrigo et al. 2007). He has used what he calls a “hot zone” approach to analyze the distribution of cut marks in the FLK Zinj assemblage (further detailed in Chapter 4), and has argued that cut marks seen on anatomical areas where flesh never survives felid consumption (hot zones) indicate primary access by hominins. This is regardless of cutmark frequency; the important indicator is the presence or absence of cut marks in these areas. “Cold zones” on the other hand, are those areas where flesh remains after felid consumption, and so cut marks in cold zone areas do not allow for inferring hominin or felid priority of access.

Documenting the presence or absence of cut marks in hot zones can allow us to assess whether hominins at Kanjera were potentially scavenging from felid kills, or whether hominins had primary access to carcass parts at Kanjera. I apply the hot zone approach to the Kanjera fauna by mapping bone regions that should not preserve flesh following felid consumption over the Kanjera GIS images for cut mark distribution. These zones are available only for the upper (humerus and femur) and intermediate (radio-ulna and tibia) limb elements, and I have only overlain them on the Kanjera GIS images when cutmarks actually occur (i.e., cut marks do not occur on every element at Kanjera). Metapodials are excluded from this hot zone analysis, as they were typically unmodified in Domínguez-Rodrigo’s (1999) study as well as in my own felid experiments (Chapter 2).

Fossil Collections

I collected data on the Kanjera South specimens at the National Museums of Kenya over the course of several months during 2011 as well as during a pilot study conducted in 2009. I examined all limb elements from bovids of all size classes from Excavations 1 and 2. I also included specimens from excavations conducted in 2009, which are reported on for the first time here. Within the total assemblage, 317 identifiable bovid limb specimens were complete enough to use in the analysis.

In order to examine potential differences in modification patterns on different sized carcasses, I sorted bovid limb fragments into 3 size categories (small, medium and large). Small (size 1) carcasses are Thomson's gazelle-sized (*Gazella* [= *Eudorcas*] *thomsonii*). Medium (size 2 through 3a) carcasses are topi-sized (*Damaliscus*). Many of these medium-sized bovids belong to the extinct genus *Parmularius*. Large (size 3b) carcasses are wildebeest-sized (*Connochaetes*). No size 4 or larger specimens were included in this analysis. Size classes follow Bunn (1982). These categories are slightly different from those used by Ferraro et al. (2013) because I have included size 2 with the medium rather than small bovids. I have chosen to divide the assemblage in this manner to facilitate comparison with my experimental assemblages, most of which are size class 2. Following the protocol of Ferraro (2007), I grouped specimens from excavations 1 and 2 together. The excavation 2 sample is smaller and only adds specimens from Bed KS-3.

There do not appear to be significant differences in the processes leading to site formation between Beds KS-1 through KS-3. Ferraro (2007) found no major shifts in faunal assemblage composition throughout the sequence, so these levels are treated the same here. The only difference is the somewhat wetter environment indicated to begin in Bed KS-3. In the GIS bone portion survivorship analyses for small and medium-sized bovids the sample size was large enough to allow me to include KS-1 and KS-2 alone. KS-1 and 2 seem to be more closely related in terms of depositional history than they are to KS-3. KS-3 contains a greater number of larger bovids, and so was included in the large bovid bone portion survivorship analysis. Due to small sample numbers for bone surface damage, KS-3 was also included in all surface damage analyses. Due to poor bone preservation in conglomerate facies (CP levels described in Plummer et al. 2009a) as well as an apparent non-behavioral depositional history (water flow), I follow Ferraro (2007) in excluding fossils from these deposits. I have included them only in bone preservation analyses of size 3b bovids, as the sample size is otherwise too small to analyze. CP specimens are not included in surface modification analyses.

I examined all bones under a strong light source using a 10x hand lens to identify surface modifications including evidence for carnivore gnawing as well as hominin-induced butchery marks and percussion damage. Bone surface modifications were identified based on published criteria (Binford 1981; Bunn 1981; Blumenschine and Selvaggio 1988; Blumenschine et al. 1996; Domínguez-Rodrigo and Barba 2006). Bone modifications at KJS had previously been jointly identified by a “round table” of three investigators (Ferraro 2007). I initially identified modifications independently, and then checked against the list of previous identifications. My identifications were in concordance with what Ferraro’s “round table” found and were not out of the small range of variation seen among the three original observers. Bone surface modifications from the 2009 excavation were assessed in the same “round table” format and checked against identifications made by J. Oliver and F. Forrest.

Experimental Collections

I have used various experimentally-modified bone collections to build models of bone preservation and damage patterns using GIS. Each of these experimental collections are described below and are summarized in Table 3.3.

Canids and Felids

I have built GIS models of bone preservation and modification patterns for large felids and canids based on feeding experiments detailed in Chapters 1 and 2. My canid sample includes 1329 bone fragments, and my felid sample includes 435 fragments derived from 46 carcasses. For the large canid experiments, bone damage patterns on both the left and right sides

Table 3.3 Summary of collections in GIS study

Collection	Carnivore Agent	Reference	Location	NISP*
Fossil				
Kanjera South		Ferraro et al. 2013	National Museums of Kenya	317**
FLK Zinj		see Chapter 4	National Museum of Tanzania	292***
Modern				
Carnivore Only	Canid	This study	Queens College	1329
Carnivore Only	Felid	This study	Queens College	435
Carnivore Only	Hyaenid	Blumenschine 1988	Rutgers University	80
Hominin→ Carnivore	Hyaenid	Blumenschine 1988	Rutgers University	138
Hammerstone only	n/a	Blumenschine 1988	Rutgers University	238
Stone tool butchered	n/a	Unpublished data	Queens College	37 bones (fragments not counted)

My own experimental assemblages are highlighted. *NISP = Number of identifiable specimens included in GIS study (this does not necessarily equal the total assemblage NISP, as only specimens identifiable to element and portion could be considered here.) These also include only limb elements.
**This includes unpublished specimens excavated in 2009, which are not included in Ferraro et al. (2013)
*** This is the number of specimens identifiable to element and with good cortical surface preservation.

were nearly identical, and so I only present the left side here. For the felid experiments, damage to both sides was also the same, but all right elements were mirrored over the left side to create a composite right/left image for each element, and also producing a larger sample size. In both the canid and felid experiments, almost exclusively size class 2 carcasses from white tailed deer (*Odocoileus virginianus*) were used.

Stone Tool Butchered

I have included cluster analysis models of cut mark distribution on an unpublished experimental assemblage of goat hind limbs that is curated in the Queens College Anthropology department zooarchaeology lab. These experiments were conducted by T. Plummer along with an undergraduate honors student (Ann Burns) with the goal of examining cut mark distribution produced by stone tools on fully fleshed limb bones. The experiments included 19 goat hind limbs that were acquired from a local butcher. A professional butcher at the shop helped to carry out the defleshing, which was conducted using quartzite flakes produced in the lab by T. Plummer. Of the 19 limbs, 13 were defleshed by the professional butcher, 5 by T. Plummer, and 1 by the student. After butchering was complete, the limbs were cleaned of any remaining pieces of flesh, and care was taken so that no further damage was done to the bones during the cleaning process. The assemblage includes 37 bones (one was unavailable for study as it had been borrowed for teaching purposes). Only the femur and tibia preserved cut marks, and so only these elements were included in the analysis. In general, the professional butcher was responsible for the most heavily cut marked bones. Of the 37 bones, 34 preserved cut mark damage. The 3 bones that did not preserve marks were butchered by T. Plummer.

Data entry into GIS was conducted by an honors student (Elizabeth Evangelou) at Queens College, who was trained by me. This is the only experimental collection for which data were not entered by me. I conducted the cluster analysis of butchery marks in ArcGIS 9.2 following the method outlined in Chapter 1 and supplementary material. The collection of hind limb bones is much larger than Blumenschine's hammerstone only experiments which included 8 femora and 6 tibiae complete enough for me to analyze using GIS. The large sample size in Plummer's experiment facilitated cluster analysis, and this experiment may more accurately reflect patterns in cut mark placement as stone tools rather than metal knives were used. Note that Table 3.3 reports a higher NISP in Blumenschine's experiments because different experimental scenarios are combined, and bones were broken by hammerstone percussion by Blumenshine after defleshing.

Blumenschine Experimental Collections

I also collected data on experimental bone assemblages created by Blumenschine (1987, 1986, 1988, 1995; see also Pante et al. 2012), which are housed at Rutgers University. These assemblages were created through feeding experiments conducted in Tanzania's Serengeti National Park and Ngorongoro Crater with spotted hyenas (*Crocuta crocuta*), and variously model carnivore-only, hominin-only and hominin-first access to carcasses. Blumenschine's assemblages have previously been studied in detail for evidence of bone damage, and my data collection consisted of re-identifying bone modification traces and inputting them into GIS to build models. Following my protocol for data collection in my experimental felid collection, I mirrored right element images over the left side to create right/left composites for each element. I entered 456 fragments into GIS out of Blumenshine's original 598 (Table 3.3). Prey carcasses for small and medium-sized bovids included Grant's gazelle (*Gazella* [=*Nanger*] *granti*), Thomson's gazelle (*Gazella* [=*Eudorcas*] *thomsonii*), and impala (*Aepyceros melampus*). Large carcasses included topi (*Damaliscus lunatus*) and wildebeest (*Connochaetes taurinus*).

Carnivore Only

Blumenschine's "carnivore only" experiments include observations on limb bones derived from carcasses observed in the wild. His original carnivore only sample included 9 assemblages. However, I have excluded two of these from my analysis due to involvement by carnivores other than spotted hyenas (SER35, which included lion gnawed and broken bones in addition to a possible hyena contribution; and SER66, which was a cheetah created assemblage). For the size 1 and 2 carnivore only experiments, hind limb fragments were all that remained, and so forelimb elements are not available for GIS models. For larger-sized carcasses, both fore and hind limbs were present. It should also be noted that the sample size is extremely small for the carnivore only hyaenid experiments, in some cases consisting of a single fragmented bone. The sample size is partly a function of a low number of assemblages and small number of bones to begin with, but also reflects the intensive damage hyenas are capable of inflicting on bones compared to canids or felids, such that they have destroyed bones to unidentifiable fragments not amenable to GIS analysis.

Hammerstone Only

Part of Blumenschine's sample, these experiments include bones defleshed with a metal knife and broken using a hammerstone and anvil technique to replicate hominin only access and marrow extraction. For the large bovid sample, no femora or tibiae were available for GIS analysis.

Hammerstone-to-Carnivore (Simulated Sites)

These experiments replicate carnivore scavenging of hammerstone broken and demarrowed bones. For these experiments, Blumenschine defleshed and broke bones using hammerstone percussion as in the hammerstone only models, but then set bones out on the landscape immediately following breakage for carnivores to feed on. Spotted hyenas are in most cases the sole scavenger of these "simulated sites," however, minor disturbance by jackals or mongooses cannot be ruled out. Bones from larger-sized bovids were available for GIS modeling, but only femora and tibiae from small bovids were complete enough to include in this analysis.

RESULTS: BONE PORTION SURVIVORSHIP

This section presents results of GIS analyses of bone portion survivorship. These analyses are fully illustrated in Appendix A. Right and left sides for each element from Kanjera are shown separately and compared against GIS models based on experimental assemblages. Small bovids in GIS analyses are size class 1 while medium include size class 2, specimens intermediate between size 2 and 3, and size class 3a.

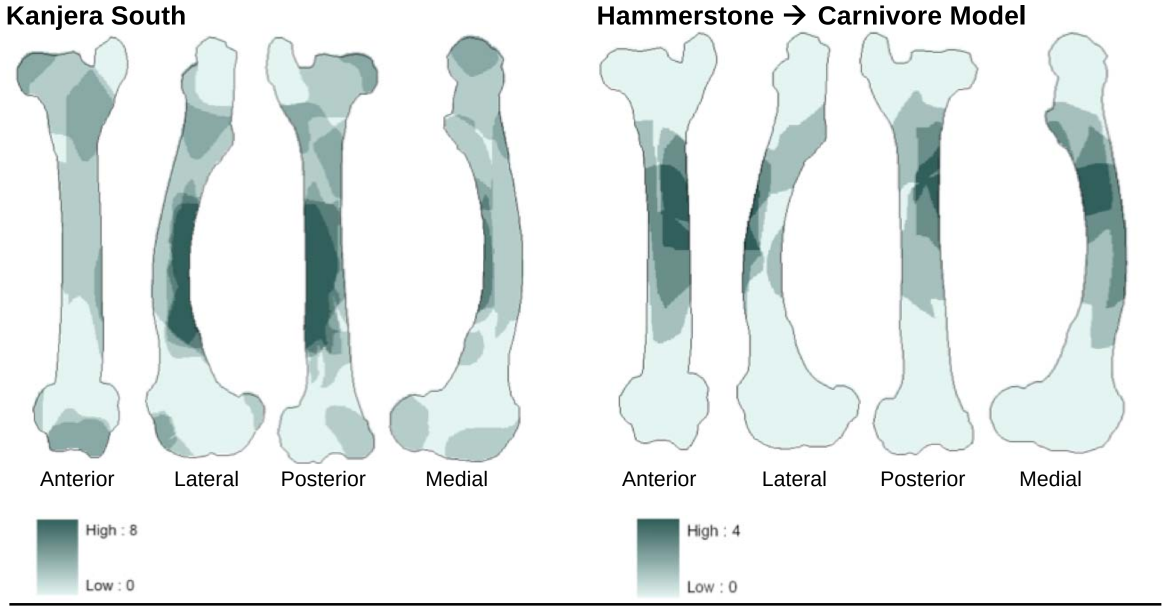
Bone Portion Survivorship – Small and Medium Bovids

Femur

The medium-sized bovids at Kanjera South show a pattern very similar to the hammerstone-to-carnivore experimental model, with a high degree of preservation in the midshaft area, and fragments that are not complete cylinders (Fig. 3.6, Figs. A.1-A.2). Epiphyses are not well preserved, although slightly better preserved than in the experimental model.

The small bovid femora are somewhat more complete and resemble more closely the hammerstone only model. The light area on the bone preservation figure for the Kanjera small bovid left side is due to small sample size (Fig. A.1), and is driven by a single juvenile fragment missing its epiphyses, but lacking carnivore gross bone damage.

Figure 3.6. Preservation of the size 2-3a left femora at Kanjera compared to Blumenschine's hammerstone → carnivore experimental model.
Note the high degree of preservation in the midshaft. See Appendix A for complete set of models.



Tibia

The medium-sized tibiae at KJS display a similar pattern of high preservation in the midshafts, deletion of the proximal epiphyses, but the distal epiphyses remain (Figs. A.3-A.4).

The small bovid tibiae display a variable pattern that is not consistent across the right and left sides. The majority of fragments show greater preservation than the medium-sized tibiae.

Metatarsal

The medium-sized metatarsals show higher preservation proximally and lower preservation more distally (Figs. A.5-A.6). It is somewhat unclear how this element might compare to experimental scenarios, as the hammerstone-to-carnivore sample consists of only a single specimen. It does not resemble the hammerstone only sample, and some carnivore involvement with the KJS remains is likely. The sample of small bovid metatarsals from KJS is small (n=5), but they are all mostly complete, save for one small proximal fragment.

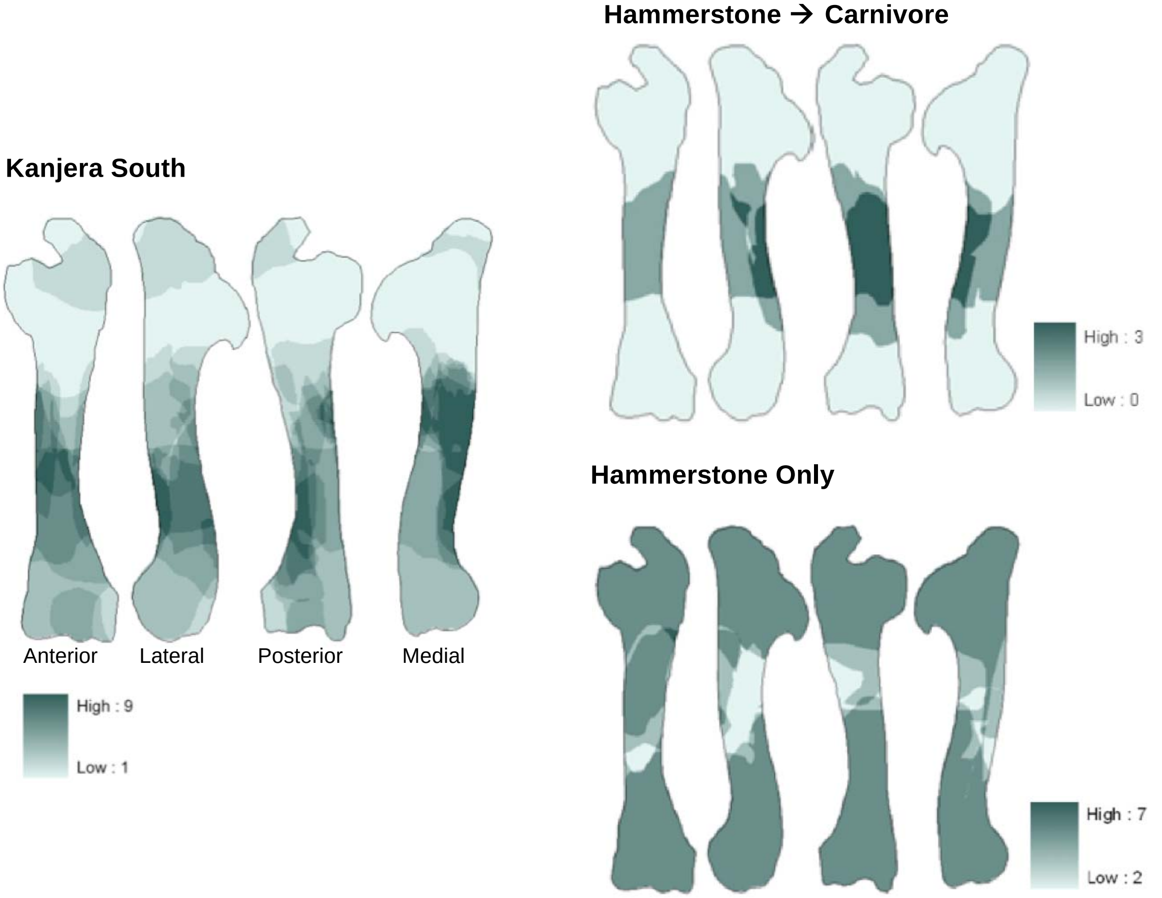
Humerus

The humerus, a meat-bearing upper limb element, shows a similar fragmentation pattern to the hammerstone models, but without the same degree of epiphyseal deletion seen in the hammerstone-to-carnivore experiments for medium-sized animals (Fig. 3.7, Figs. A.7-A.8). The pattern is similar for the small animals, however, some (see size 1 left side) show a greater degree of epiphyseal deletion.

Radius

The medium-sized radii at KJS are highly fragmented, but preservation is highest at the proximal and distal ends – a preservation pattern very closely resembling the hammerstone only model (Fig. A.9-A.10). The small bovid radii are highly fragmented, and preserve almost exclusively the proximal ends.

Figure 3.7. Preservation of the size 2-3a left humeri at Kanjera compared to Blumenschine's hammerstone → carnivore and hammerstone only experimental models.
Note similarity of KJS to the fragmentation pattern seen in these hammerstone broken models, but without the same degree of epiphyseal deletion seen in the hammerstone → carnivore model. See Appendix A for complete set of models.



Ulna

Preservation of the medium-sized ulnae at KJS resembles the carnivore-only models, except that the shaft in the KJS specimens shows greater destruction (Figs. A.11-A.12). The olecranon process is moderately destroyed. Carnivore involvement is perhaps more likely to be expected for this element, as it is not marrow bearing. The small bovids at KJS are better preserved, with more intact olecranon processes, resembling more closely the hammerstone only model. This discrepancy in destruction between small and medium bovids, with the small animals displaying less fragmentation than the larger, is opposite the pattern we might expect in a carnivore ravaged assemblage.

Metacarpal

Both medium and small metacarpals from KJS are highly fragmented (Fig. A.13). However, there is high representation of fragments across all bone areas, though preservation is highest at the proximal end. Smaller animals, again, show somewhat higher preservation. The patterns at KJS follow the pattern from the hammerstone only models (Fig. A.14). The hammerstone-to-carnivore model is difficult for comparative purposes as it is comprised of only a single fragment.

Bone Portion Survivorship – Large Bovids

The large bovids (large considered here as wildebeest-sized or larger, size 3b) from KJS are less well represented than small and medium bovids, and are compared in Figs. A.15-A.20 with GIS models based on Blumenschine’s experimental assemblages. Hammerstone only models were not available for the femora and tibiae. I use Blumenschine’s spotted hyena damaged assemblage for the carnivore only model, as my own experiments with canids and felids did not contain enough large animals.

Femur

The large bovid femora at KJS (Fig. A.15) are highly fragmented and show highest preservation in the midshafts. The deleted distal ends resemble the carnivore only model, however, the sample sizes for these experimental models are so small they are difficult to use for comparative purposes. Although preservation is highest in the midshaft, the high fragmentation level is suggestive of hominin involvement as well. A hammerstone only model is not available for large femora.

Tibia

The single large tibial fragment from KJS is a posterior midshaft fragment (Fig. A.16). It is difficult to compare to experimental models, and a hammerstone only model is lacking for large bovids. However, this fragment is broken in a way suggestive of hammerstone fracture. Carnivore tooth scores are present on this fragment as well.

Metatarsal

Large bovid metatarsals at KJS (Fig. A.17) are highly fragmented and only proximal and distal ends remain. Presence of the epiphyses suggests negligible carnivore involvement, while complete fragmentation of the midshafts is suggestive of hammerstone damage. The midshafts are likely present as unidentifiable small fragments that could not be placed accurately on the GIS template.

Humerus

Both right and left humeri at KJS preserve midshaft portions and lack epiphyses (Fig. A.18). It is difficult to determine which model this may fit due to small sample sizes in the humerus models. The overall preservation pattern resembles the carnivore model, but the fragmentation pattern resembles that of the hammerstone-to-carnivore model, where fragment do not preserve the entire shaft circumference. Further, the presence of percussion damage on the humeral fragments indicates hominin involvement here (Fig. 3.8).

Figure 3.8. Example of percussion notches on large bovid humerus (#7379).
Left side is cortical view, right side is medullary view.

Radio-Ulna

The large radio-ulnae at KJS (Fig. A.19) preserve only the proximal ends (radius proximal end is preserved in 2 specimens, proximal ulna preserved in 1 specimen). The grease-rich cancellous bone of the proximal end is normally destroyed by carnivores. The KJS pattern does not resemble the carnivore only GIS model; however, for the large bovids this model consists of only 2 bones, which complicates comparison. The preservation seen in the proximal end and high degree of fragmentation make the hammerstone only or hammerstone-to-carnivore model closer matches. The distal ends in the KJS radio-ulnae are missing, which may suggest some carnivore involvement.

Metacarpal

The KJS large bovid metacarpals (Fig. A.20) preserve only distal ends, while proximal ends are destroyed. The experimental models for large metacarpals are not well differentiated due to their small sample size.

Summary of Bone Portion Survivorship Patterns

Overall, the limbs from small carcasses are better preserved than those from medium-sized carcasses. This pattern seems to rule out density-mediated destruction by carnivores, as the opposite pattern would be expected in that case, with smaller elements being differentially destroyed. Instead, these differences likely reflect differing behavioral strategies practiced by hominins regarding the transport of small and medium-sized carcasses to Kanjera. This is an interpretation Ferraro et al. (2013) have made as well, based on analysis of skeletal part frequencies. An alternate interpretation could be that size 3b specimens were more intensively processed following transport.

One important difference between the smaller (size 1) and medium (size 2-3a) specimens from KJS should be noted. Some GIS models for the KJS small bovid limbs that have epiphyseal sections missing may superficially resemble the carnivore only experiments. However, many of these are actually juvenile specimens missing their unfused epiphyses. These specimens account for 13% of the limb bones included in this GIS analysis (42 out of 317 limb bone fragments had at least one unfused epiphysis). Further, of those juvenile specimens, only 4 fragments (<10%) display evidence of carnivore gnawing, indicating carnivore involvement is not the main factor driving low epiphyseal representation in relation to shaft representation.

RESULTS: BONE MODIFICATION PATTERNS

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

In the GIS analyses below, due to a low number of individual modifications per element, I have displayed modifications together for small and medium bovids (size 1-3a), but separate out the large bovids (size 3b). Analyses are fully illustrated in Appendix B. In experimental models where large enough sample sizes exist, I present GIS density analyses. Density analyses indicate bone portions where significantly dense clusters of modifications occur (see Chapter 1 and Chapter 1 and supplementary material to Chapter 1 for a full description of this method). Where sample sizes are small, density analyses are not meaningful, and so I present plots of individual marks on GIS element templates instead. This is the case for the Kanjera assemblage, as well as the sample for hominin-induced modifications from Blumenschine's experiments. Carnivore damage analyzed includes tooth pits, punctures, and scores. Hominin damage includes cut marks, percussion marks (including percussion pits and striae), and percussion notches.

The patterns and specific damages discussed below are those that I was able to locate reliably on GIS element templates. In other words, damage that occurs on fragments with anatomical landmarks which allow accurate placement on a template of a complete element. The GIS images represent plots of modifications that could be reliably assigned locations on element

Table 3.4. Fragment count and bone surface modification frequencies for all specimens used in GIS analysis broken down by skeletal element and size class.

These are combined Beds KS-1–KS-3. Numerator is total number of tooth marked specimens, denominator is total number of specimens for each skeletal element, and percentages are in parentheses. This includes 28 unpublished specimens excavated in 2009, which were not included in Ferraro et al. (2013). Bone damage frequencies reflect frequencies only in the portion of the KJS assemblage used in the GIS analysis. See Ferraro (2013) for complete frequency data. Specimens from CP levels were not counted except for large bovid specimens, as the sample size would otherwise be too small. Small = size 1, medium = size 2-3a, large = size 3b-4. All beds combined. Percussion marks include pits, striae, and notches. Large ulnae were fused radio-ulnae and counted as radii.

	Tooth marks	**Cut marks**	**Percussion Marks**
Humerus			
Small	3/18 (16.7)	0/17 (0)	0/17 (0)
Med.	8/45 (17.7)	0/45 (0)	3/45 (6.7)
Small + Med.	11/63 (17.5)	0/62 (0)	3/62 (4.8)
Large	1/5 (20)	1/5 (20)	1/5 (20)
Total	12/68 (17.6)	1/67 (1.5)	4/67 (6)
Radius			
Small	1/8 (8.9)	0/8 (0)	1/8 (1.3)
Med.	4/43 (9.3)	0/43 (0)	2/43 (4.7)
Small + Med.	5/51 (9.8)	0/51 (0)	3/51 (5.9)
Large	1/5 (20)	2/5 (40)	1/5 (20)
Total	6/56 (10.7)	3/56 (5.5)	4/56 (7.1)
Ulna			
Small	0/5 (0)	0/5 (0)	0/5 (0)
Med.	1/11 (9.1)	0/11 (0)	1/11 (9.1)
Small + Med.	1/16 (6.3)	0/16 (0)	1/16 (6.3)
Large	-	-	-
Total	1/16 (6.3)	0/16 (0)	1/16 (6.3)
Metacarpal			
Small	1/8 (1.3)	0/8 (0)	0/8 (0)
Med.	6/27 (22.2)	1/27 (3.7)	0/27 (0)
Small + Med.	7/35 (20)	1/35 (2.9)	0/35 (0)
Large	1/3 (33.3)	0/3 (0)	0/3 (0)
Total	8/38 (21.1)	1/38 (2.6)	0/38 (0)
Femur			
Small	4/14 (28.6)	1/14 (7.1)	0/14 (0)
Med.	2/31 (6.5)	2/31 (6.5)	3/31 (9.7)
Small + Med.	6/45 (13.3)	3/45 (6.7)	3/45 (6.7)
Large	1/7 (14.3)	0/7 (0)	0/7 (0)
Total	7/52 (13.5)	3/52 (5.8)	3/52 (5.8)
Tibia			
Small	0/12 (0)	0/12 (0)	0/12 (0)
Med.	5/44 (11.4)	4/44 (9.1)	6/44 (13.6)
Small + Med.	5/56 (9)	4/56 (7.1)	6/56 (7.1)
Large	0/2 (0)	0/2 (0)	0/2 (0)
Total	5/58 (8.6)	4/58 (6.9)	6/58 (10.3)
Metatarsal			
Small	1/6 (16.6)	2/6 (33.3)	0/6 (0)
Med.	4/21 (19)	1/21 (4.8)	1/21 (4.8)
Small + Med.	5/27 (18.6)	3/27 (11.1)	1/27 (3.7)
Large	0/3 (0)	0/3 (0)	0/3 (0)
Total	5/30 (16.6)	3/30 (10)	1/30 (3.3)
Grand Total	44/318 (13.8)	15/318 (4.7)	19/318 (6)

templates, and do not reflect total bone surface modification counts. Ferraro (2007) and Ferraro et al. (2013) have analyzed unidentifiable fragments in detail, and report complete bone surface modification frequency data. Bone surface modification data included in this GIS analysis are summarized in Table 3.4, and individual specimens bearing modifications are listed in Appendix C. I discuss here the location of particular surface modification clusters that are potentially informative regarding the order of access of hominins and carnivores to carcasses at Kanjera in light of GIS experimental models.

Patterns of Carnivore Damage – Small and Medium Bovids

Hindlimb

The small and medium-sized bovid femora from KJS show a random distribution of carnivore tooth marking, as do the tibiae and metatarsals (Figs. B.1-B.3). This lack of identifiable tooth marking pattern is probably a reflection of the low overall tooth mark frequencies, and an indication of low carnivore involvement at the site.

Forelimb

On the forelimb, the pattern on the humeri (Fig. B.4) most closely resembles the carnivore only experiments; however, given the known attraction of carnivores to grease-filled epiphyseal portions (e.g., see canid tooth mark distribution in Fig. B.4), I predict that if the sample size for the hammerstone-to-carnivore model was increased (it only consists of 3 elements), a cluster of tooth marking may appear on the distal condyle similar to what is seen at KJS. Further experiments are needed to investigate this.

The radius and ulna from KJS (Figs. B.5-B.6) show some tooth marking on the epiphyses. The placement of tooth marks on these elements does not contradict the carnivore only model, but a hammerstone-to-carnivore model is not available for these elements.

However, if carnivores had sole access to these elements, I would predict more intensive damage to the olecranon process. This grease-filled portion is attractive to carnivores, and its low density makes it easily destroyed (note this portion is typically present in the KJS ulnae: see Fig. A.11).

Finally, the metacarpals from KJS (Fig. B.7) show tooth marks in a seemingly random distribution across the element, somewhat resembling the distribution in the carnivore only model. The hammerstone-to-carnivore model, however, consists of only a single specimen, so may not be a realistic model.

Patterns of Carnivore Damage – Large Bovids

The only large bovid element showing carnivore damage that I was able to map reliably onto the GIS image template was the radio-ulna. Tooth marks appear mainly on the epiphyses in a single large bovid radio-ulna specimen from KJS. There is no hammerstone-to-carnivore experimental model to compare this with, but the distribution of tooth marks at KJS does not resemble the carnivore only hyaenid model which displays a more even distribution of tooth marking (Fig. 3.9). Complete GIS models for experimental collections based on carnivore modification to large bovids are presented in Appendix B, Figs. B.8-B.9.

Patterns of Hominin Damage – Small and Medium Bovids

Hindlimb

Hominin-induced damage to the Kanjera femora includes cut marks as well as percussion marks and notches. Similar to the hammerstone-to-carnivore model, cut marks do not appear on the distal end (this is because distal ends were consumed by carnivores in the model and were no longer present) (Fig. A.15). When using Domínguez-Rodrigo’s hot zone framework to assess cut mark distribution, all but one of the cut marks found on the KJS femora occur in hot zones (Fig. 3.10). The single cut mark occurring in a cold zone is on the femoral head and shows characteristics of a disarticulation mark rather than a defleshing mark (Domínguez-Rodrigo 1997; Nilssen 2000).

Compared to the cluster analyses of experimental models of bones defleshed using stone tools (Fig. 3.11), some of the KJS cut marks occur in areas where marks clustered in experiments, but not always. These butchery experiments model defleshing, not disarticulation, and this difference may reflect disarticulation activities in addition to defleshing at KJS.

Most cut marks on small and medium bovid tibiae occur in hot zones as well. In terms of the hot zone approach, it is the location of cut marks that is most informative because these indicate flesh removal, where percussion marks indicate bone breakage after defleshing, and are thus less informative about timing of access. The KJS tibiae also preserve numerous percussion marks and percussion notches. The placement of these marks, however, occurs mostly on the posterior aspect, rather than on the medial and lateral aspects as in both the hammerstone only and

Figure 3.9. Distribution of tooth marking on the large bovid radio-ulnae at Kanjera South and in Blumenschine's experimental carnivore-modified assemblage.
Tooth marks at Kanjera appear only on specimen (#13336). n = the NISP bearing tooth marks.

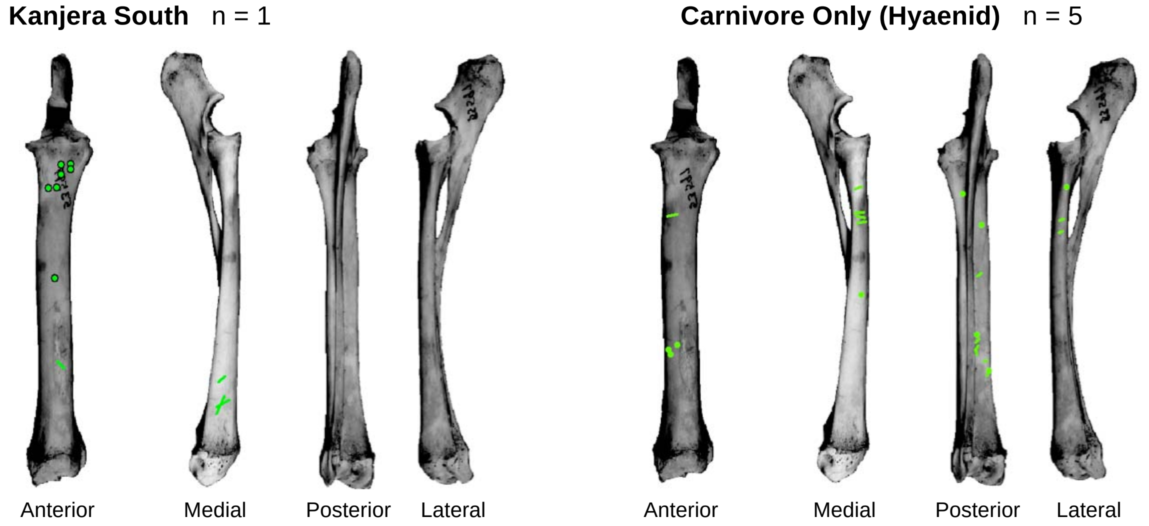


Figure 3.10. Domínguez-Rodrigo's "cold zones" overlain on the KJS small bovid hominin modifications. a. femur, b. tibia. Note cut marks occur almost exclusively in hot zones.

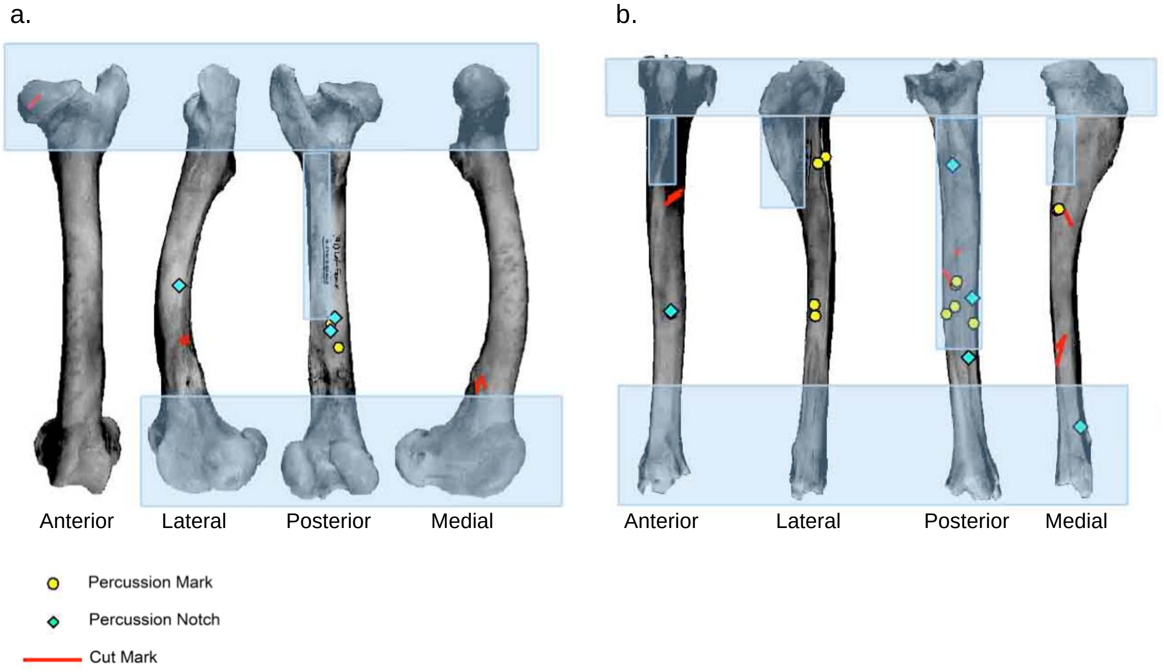
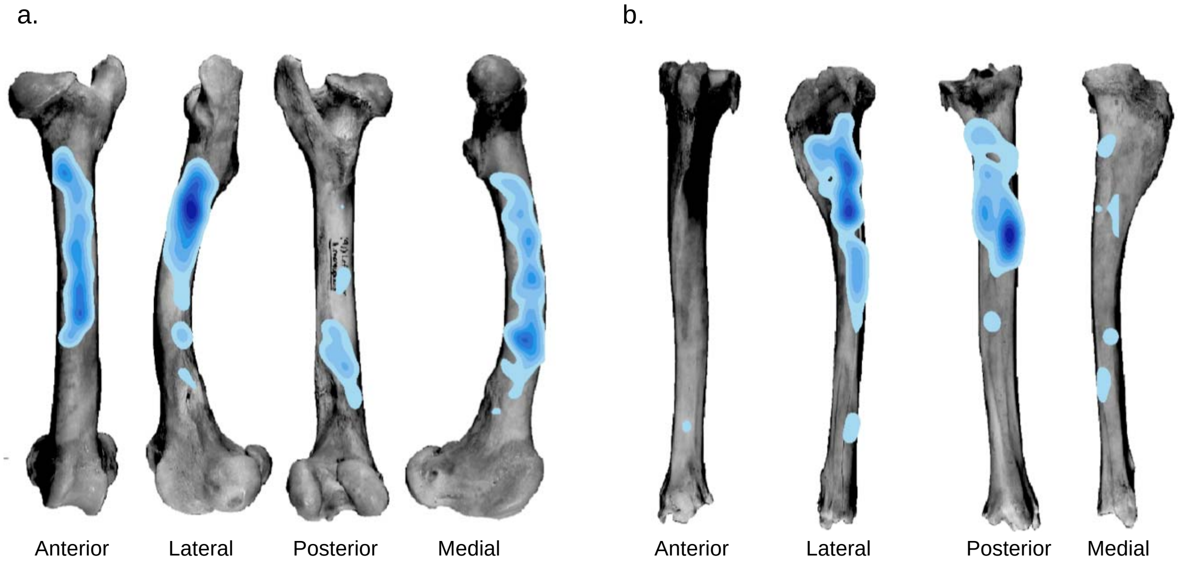


Figure 3.11. Cluster analysis of cut marks from stone tool butchered experimental assemblage. Experiment was conducted on fully fleshed, articulated goat limbs by an experienced butcher. a. femur, b. tibia. Darkest blue areas indicate areas of highest cut mark clustering.



hammerstone-to-carnivore models. This suggests that hominins at Kanjera were orienting the tibiae differently during percussion than Blumenschine did in his experiments.

Small and medium bovid metatarsals at KJS display both cut marks and percussion notches, although the intensity is somewhat less in the KJS metatarsals than in both comparative experimental models.

Forelimb

Cut marks do not occur on the small and medium bovid humeri, radii or ulnae examined in this study, although one humeral shaft that could not be placed on a GIS template was identified as cut marked in Ferraro's study (Ferraro 2007, Table 9). Percussion damage does occur on the radii (Fig. B.14). Hominin-induced damage is more extensive in both experimental models, than is seen at KJS.

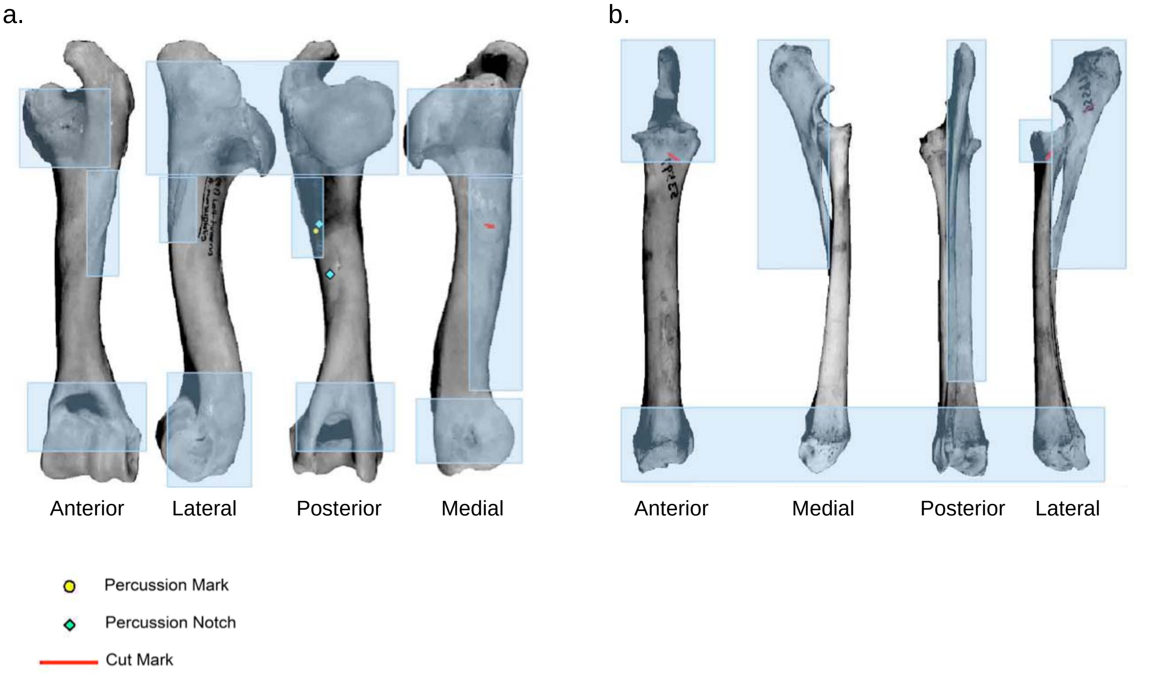
Finally, the metacarpals at KJS shows a single episode of cut marking on the posterior distal metaphysis (Fig. B.16). There is no percussion damage visible on metatarsals.

Patterns of Hominin Damage – Large Bovids

The only hominin-induced damage visible on size 3b bovids at KJS is on the forelimbs. Cut marking on the Kanjera humeri occurs in cold zones (Fig. 3.12). The one cut mark that I was able to place on the GIS template occurs directly on the insertion point for *teres major*, and could potentially indicate early access. The hammerstone only model for small and medium bovids also has cut marking medially on the *teres major* insertion.

The proximal radio-ulnae have cut marks that occur in cold zones, and are thus uninformative regarding hominin order of access. Hominin-induced damage does occur on other large (size 3-4) bovid specimens (at a frequency of 0-25% depending on observer and Bed; see Ferraro 2007, Appendix 22a-c), but I was unable to place these marks reliably on element templates. Complete GIS models for experimental collections based on human butchery and hammerstone breakage of large bovid limbs are presented in Appendix B, Fig. 17.

Figure 3.12. Domínguez-Rodrigo's "cold zones" overlain on the KJS large bovid hominin modifications. a. humerus (n = 2), b. radio-ulna (n = 2).



DISCUSSION

Results of the GIS analyses outlined above support prior interpretations of the Kanjera South archaeofauna (Ferraro 2007; Plummer 2009; Ferraro et al. 2013), which suggested that hominins had early access to relatively complete small bovids, and at least occasional access to larger bovids perhaps acquired through a mix of aggressive and passive scavenging.

Small and Medium-Sized Bovids

Overall patterns of bone portion survivorship for small and medium bovids at Kanjera exhibit a fracture pattern most consistent with the hammerstone only experimental models. Limbs of small and medium-sized bovids show some degree of epiphyseal deletion, but deletion is not to the same extent as is seen in Blumenschine's experimental hammerstone-to-carnivore models. The fact that carnivores were not completely consuming the epiphyses indicates a lower degree of competition in the Kanjera ecosystem than was present in Blumenschine's experiments. It should be noted that Blumenschine's experiments were conducted in the Serengeti and Ngorongoro crater, which are highly competitive environments (Kruuk 1972; Schaller 1972; Tappen 1995, 2001), and his experimental models reflect this.

The limbs from the small carcasses overall are better preserved than those from medium-sized carcasses. This pattern is interesting, and seems to rule out carnivore-induced density-mediated destruction, as the opposite pattern would be expected in that case, with carnivores destroying smaller elements more thoroughly. Studies have shown that smaller-sized carcasses are normally at greater risk for destruction than medium-sized carcasses, particularly in grassland contexts where they are typically completely consumed by lions and/or hyenas within several hours after death (Blumenschine 1987; Domínguez-Rodrigo 2001).

Rather than suggestive of a carnivore accumulated assemblage, the preservation differences seen between the small and medium-sized carcasses instead likely reflect differing behavioral strategies practiced by hominins at KJS regarding size-related differences in transport behavior or processing intensity. This is an interpretation Ferraro et al. (2013) have also advanced based on differing skeletal part frequencies seen between smaller and larger carcasses. Ferraro and colleagues found a high representation of all skeletal elements for smaller bovids, likely reflecting access to complete carcasses. For medium-sized animals, they found a high representation of meaty limb bones as well as head elements. They argued this may reflect separate foraging activities in which hominins might have acquired limbs of medium-sized animals early on, but heads may have been passively scavenged for their internal food resources (i.e., brain tissue). I am presuming hominin agency in accounting for the accumulation of bones at KJS, as Ferraro (2007) has shown that the assemblage composition does not resemble a background landscape scatter, and the presence of cutmarks and percussion damage on the bones further illustrates hominin agency.

Relative to the carnivore only experimental models, the high preservation of epiphyses in small and medium bovids at KJS indicates carnivores were not forming or greatly modifying the assemblage. Epiphyses are less well represented in the size 1 bovids compared to size 2-3a bovids. However, 24% of the size 1 bovids (17/72 specimens in this study) were juveniles missing at least one unfused epiphysis. Given this, carnivores are not likely to account for the lower epiphyseal representation in size 1 bovids. The low frequency and random distribution of carnivore tooth marking in the small and medium bovid limbs is consistent with low carnivore involvement at the site, and suggests secondary access to carcasses by carnivores. Although the tooth mark evidence indicates carnivores were present at Kanjera and contributed to site formation, there seems to have been low on-site competition over carcasses.

The occurrence of cut marks in hot zones on the meaty hindlimb elements at KJS suggests hominins had primary access to these carcasses. Flesh typically does not survive felid consumption in hot zones, so there would have been no flesh left to remove in these areas if hominins were scavenging from felid kills. Also, the presence of percussion marks and notches and the high degree of fragmentation of most of the long bones indicate hominin exploitation of within-bone resources.

Large Bovids

The tooth marking data for size 3b bovids is more difficult to interpret, as placement on the GIS templates was only possible for a single radio-ulna specimen which was highly tooth marked. This is consistent with interpretations of KJS suggesting hominins may have been scavenging at least some of the larger bovid remains, and thus larger bovids may be expected to show heavier tooth marking. Hominin involvement with large bovids is evidenced by cut and percussion damage to the humerus, although cut marks are not in hot zones in this case.

The difference in bone modification patterns seen between the small and large bovids may be related to differences in carcass acquisition strategies as Ferraro et al. (2013) have suggested. Ferraro's argument is based on differences in skeletal element representation between small and larger-sized bovids, but on an assemblage-wide level, they found there is no significant difference between tooth mark frequencies or cut mark frequencies between size classes. The data presented here on specific patterns of bone modification seen in small versus larger bovids are not inconsistent with Ferraro et al.'s interpretation that hominins may have been scavenging at least some of the larger bovid remains.

CONCLUSIONS

In summary, the interpretation of the Kanjera South zooarchaeological record based on this GIS analysis supports other interpretations that have been made of the site, namely that Oldowan hominins had early access to small bovids and were habitually processing carcasses at this focal point on the landscape. Cut marks occur in hot zones on bones where flesh typically does not survive felid consumption, indicating early access to flesh by hominins. Further, the presence of percussion marking and high degree of fragmentation of the long bones indicate marrow processing by hominins. Distribution of these hominin-induced damages are not unlike GIS models based on experiments modeling early hominin access.

Carnivores were also involved in modifying carcasses to some extent, but do not appear to have been the agent of transport. This is indicated by the high survivorship of elements from small carcasses, which would likely have been completely consumed by carnivores if they had initial access. Low tooth mark frequencies and their random distribution are consistent with low carnivore involvement and suggests secondary access by carnivores. Relative to GIS models of carnivore only scenarios, the higher preservation of epiphyses at KJS suggests carnivores were not forming or greatly modifying the assemblage. Although carnivores were present, there seems to have been lower on-site competition at Kanjera compared to other Oldowan sites, notably FLK Zinj. This will be explored further in Chapter 4.

Taken together, this GIS evidence suggests, in agreement with other lines of evidence, that hominins had relatively early access to carcasses at Kanjera and may have been hunting the smaller animals. If this is the case, Kanjera South may provide the oldest evidence of hunting in the fossil record, and it thus lies at a critical juncture in documenting one of the major adaptive changes in our genus.

CHAPTER 4. A GIS Image Analysis of Bone Surface Modification Patterns in the FLK 22 (FLK Zinj) Assemblage, Olduvai Gorge, Tanzania

ABSTRACT

This paper presents a taphonomic examination of the FLK Zinj bovid fauna using a GIS image analysis technique. Patterns of bone portion survivorship as well as stone tool and carnivore damage are analyzed within a comparative framework of experimental models in order to assess whether Oldowan hominins at this site had early access to fleshed carcasses through hunting or active scavenging, or late access to largely defleshed carcasses through passive scavenging. Results are then compared with GIS image analyses of the fauna from Kanjera South, an Oldowan zooarchaeological assemblage of similar age. Results of these analyses support an interpretation that hominins had early access to fleshed carcasses at FLK Zinj, particularly of smaller prey, which may have been acquired through hunting. Damage patterns on larger carcasses are more difficult to interpret, but are not inconsistent with early access (hunting or aggressive scavenging).

Analysis of carnivore tooth mark frequencies on the FLK Zinj bovid fauna reported here corroborate those cited by Domínguez-Rodrigo and colleagues (2007), lending additional support to an early access scenario for hominins. Based on bone surface damage frequencies, the fauna at FLK Zinj is more heavily processed by both hominins and carnivores than the zooarchaeological assemblage from Kanjera South. However, patterns of bone fragmentation are similar at both sites. Similarity in fragmentation patterning but differing levels of bone surface damage may indicate hominin behavioral differences related to carcass processing at these two sites.

INTRODUCTION AND BACKGROUND: HISTORY OF ZOOARCHAEOLOGICAL RESEARCH AT FLK ZINJ (OLDUVAI GORGE, TANZANIA)

The majority of research on Oldowan hominin carcass acquisition strategies has been based on the well-preserved fauna from the FLK Level 22 site (also known as FLK Zinj) from Bed I, Olduvai Gorge. This site was originally excavated by Louis and Mary Leakey following their discovery of the *FLK Zinjanthropus* (now known as *Paranthropus) boisei* hominin cranium. The FLK, or Frida Leaky Korongo excavation (named after Louis Leakey’s first wife), exposed a number of stratigraphic levels containing stone artifacts and bone to a depth of 12 m

(Potts 1988). However, level 22 at FLK is notable because it is the largest preserved ancient land surface of any of the Bed I sites at Olduvai.

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

Dating to around 1.84 Ma, this site contains approximately 60,000 faunal specimens (3,500 of which are identifiable to at least skeletal part) representing a minimum of 48 large mammal carcasses (most of them bovid) as well as over 2,500 Oldowan stone artifacts (Leakey 1971; Bunn and Kroll 1986; Potts 1988; Domínguez-Rodrigo et al. 2007). Because of the large size and exceptional preservation of the collection, the FLK Zinj assemblage has been used extensively in reconstructions of early hominin behavior. This site served as the basis for Mary Leakey's (1971) "living floor" hypothesis, which envisioned the site a base camp from which hominins dispersed and returned to on a daily basis and which would have been the center of social activities. In the decades following Leakey's original interpretation, the site has been variously interpreted as a "home base" or "central place" at which food sharing activities may have taken place (Isaac 1978, 1981, 1983; Bunn 1982; Bunn and Kroll 1986; Rose and Marshall 1996), a place where carcasses or carcass parts obtained through hunting or more aggressive, confrontational scavenging were deposited (Bunn and Ezzo 1993; Domínguez-Rodrigo and

Pickering 2003), and a carcass processing locale where stone for making tools was cached and carcasses were repeatedly butchered over time (Potts 1988). The site has also been used to support behavioral models of passive scavenging, and it has been interpreted as a woodland refuge where hominins may have brought scavenged carcass remains (Blumenschine 1991; Blumenschine et al. 1994). The history of zooarchaeological research at FLK Zinj is summarized in more detail in the sections below.

Despite these numerous previous interpretations of site function at FLK Zinj, there is currently no consensus among researchers regarding the mode of carcasses acquisition by hominins at the site. The purpose of this paper is to add additional analyses using a new methodology (GIS image analysis) in order to address this question. Results from this suggest that hominins had early access to carcasses at FLK Zinj and were not confined to passive scavenging.

Skeletal Part Frequency Studies at FLK Zinj

Skeletal part frequencies initially occupied a central role in reconstructions of hominin carcass acquisition and site formation at FLK Zinj. Skeletal part profiles were seen to represent differing patterns of carcass part accumulation by hominins or carnivores. These studies were based on the ‘schlepp effect’ model of Perkins and Daly (1968), which described a pattern of differential transport of carcass parts depending on their availability and nutritional value. Typically, the axial skeleton is expected to remain at the death site because it is less nutritionally valuable, while the meat and marrow rich limbs are expected to be preferentially transported away from the death site (Bunn and Kroll 1986; Domínguez-Rodrigo and Pickering 2003).

Lewis Binford conducted the first study of skeletal part frequencies at several Olduvai sites based on Leakey’s preliminary report of the data and on his own actualistic studies of assemblages from North America (1981, 1988). He concluded that the Olduvai sites did not represent living floors, but were likely created by carnivores. He envisioned hominins as late scavengers of carnivore kills obtaining only marginal portions of carcasses. He cited a low frequency of meat bearing limb bones at FLK Zinj as evidence that the assemblage was a carnivore kill site subsequently scavenged by hominins for marrow (Binford 1981).

In addition to performing analyses with a provisional dataset based only on field observations, Binford's interpretation was marred by his decision to include only limb portions retaining epiphyses in his analysis and to ignore shaft fragments. In contrast, Bunn and Kroll (1986) performed a detailed, lab-based study of the prepared fossils that included long bone shafts. They found the assemblage at FLK Zinj was actually dominated by limb bones, with meaty elements (humerus, radio-ulna, femur, and tibia) being more abundant than non-meaty elements (metapodials). Furthermore, when elements were sorted into different size groups, they found a consistent representation of all limb elements for smaller animals, while a higher ratio of meaty limb bones relative to non-meaty limb bones was found for larger animals. Bunn and Kroll argued these skeletal element profiles provided evidence for repeated transport of carcasses by hominins to a favored place, and the abundance of cut marks on meaty limb bones indicated systematic butchery and significant meat consumption by hominins. They postulated that early access may have been achieved through confrontational scavenging of larger carcasses and possibly hunting of smaller animals. In later work, Bunn (2001) gave additional support to this argument by documenting a similarity in anatomical patterning of cut marks between the FLK Zinj assemblage and bone refuse from carcasses processed by modern Hadza hunter-gatherers of Tanzania.

Faith et al. (2009) approached the issue of skeletal element abundance and carcass transport at FLK Zinj using the Shannon evenness index. This statistic measures the evenness of the distribution of high survival skeletal elements in an assemblage in relation to their proportion in a complete carcass (Faith and Gordon 2007). High survival elements are those most likely to resist destruction, particularly carnivore ravaging, and include dense elements with thick cortical walls such as the long bones and denser portions of the cranium and mandible. The evenness index can indicate the degree of selectivity in carcass transport by foragers or carnivores (i.e., whether whole carcasses or portions of carcasses were transported). Faith et al. (2009) found a high evenness in the FLK Zinj assemblage for both small and large bovids, suggesting transport of relatively complete carcasses to the site. Compared to the lower evenness of skeletal element profiles at Middle Stone Age sites where hominins seem to have more selectively transported carcass parts, the FLK Zinj values instead suggest short distance transport of whole carcasses. Faith et al. argued that the evidence suggests FLK Zinj was a locality at which hominins regularly deposited carcass remains which they acquired nearby. They suggested FLK Zinj may have been in close proximity to localities where hominins had routine access to prey, which they may have transported to and shared at a home base (sensu Isaac 1978).

An alternate variable that may factor into the explanation for the pattern of relatively complete large carcasses seen at FLK Zinj is the number of individual hominins involved in transporting carcasses. A large group of individuals carrying a carcass would make transport of heavy carcasses over longer distances more feasible. This idea has not been fully explored, but may be impossible to test archaeologically.

While studies of skeletal part frequencies can be informative, it has become apparent that taphonomic agents and differential preservation of skeletal elements in fossil assemblages can complicate interpretations of the degree of hominin or carnivore involvement at a site. For example, some researchers have shown that large carnivores (particularly hyenas) can also create assemblages dominated by limb elements similar to sites such as FLK Zinj because they preferentially consume grease-rich vertebrae and ribs (Binford 1981; Capaldo 1997, 1998a,b). This has led other researchers to question the usefulness of skeletal part frequencies for identifying the agent responsible for site formation (Blumenschine 1986c, 1988; Oliver 1994). Recognizing that skeletal part frequencies alone are not sufficient to interpret sites, subsequent research has focused on the use of actualistic or experimental models of site formation in modern ecosystems as well as more detailed study of bone damage patterns diagnostic of hominin or carnivore involvement.

Application of Experimental Models to Interpret the FLK Zinj Taphonomy

Blumenschine's Three-Stage Model

Pioneering actualistic work by Blumenschine (1987) assessing carcass availability in modern East African environments led to his proposal of a dry season scavenging niche for early hominins (see also Foley 1987). This idea was based on the relatively predictable availability of abandoned felid kills in riparian woodlands during the dry season in the Ngorongoro and Serengeti ecosystems of Tanzania. Subsequent experimental work by Blumenschine (1995), Capaldo (1997, 1998a,b) and Selvaggio (1994a,b, 1998) was conducted in order to determine patterns resulting from differential access to carcasses by carnivores and humans. These experimental assemblages (further detailed in Chapter 3) were then used as a referential framework with which to compare the FLK Zinj assemblage. Based on this work, Blumenschine (1995) and Selvaggio (1998) suggested a three-stage model of carcass access at FLK Zinj, in which hominins scavenged bones from defleshed felid kills and processed them for marrow, and hyenas subsequently scavenged the remaining bones (largely long bone epiphyses and axial elements) after they were abandoned by hominins. This model was based on several classes of taphonomic data. Their finding of a high frequency of tooth marks on long bone midshafts was interpreted to reflect initial defleshing by felids, which do not have jaws adapted for bone cracking. They argued that hammerstone percussion marks seen on the FLK Zinj long bones are indicative of hominin marrow processing, and that cutmarks reflect the removal of flesh scraps surviving felid consumption. Finally, they argued that the low proportion of epiphyses and axial elements indicated that these elements were scavenged by bone-crunching hyenas following hominin demarrowing of long bone shafts.

Taphonomic Work by Domínguez-Rodrigo – Biochemical Marking

Domínguez-Rodrigo and colleagues (Domínguez-Rodrigo 1997; Domínguez-Rodrigo and Pickering 2003; Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo et al. 2007) have reanalyzed the carnivore tooth mark frequencies in the FLK Zinj assemblage. They argued that some modifications on long bone surfaces that had been identified as tooth marks by Blumenschine (1995) were actually produced by biochemical processes. They conducted experimental studies on the effects of fungus growth on modern bone and argued that the irregular grooved surface it creates on bone resembles carnivore tooth marking. When the authors reanalyzed the FLK Zinj bones, they identified tooth marks on less than 20% of the bones originally identified as tooth marked by Blumenschine. They argued that Blumenschine’s tooth mark frequencies were inflated because he had frequently misidentified biochemical marks as tooth marks (Domínguez-Rodrigo et al. 2007).

Domínguez-Rodrigo et al. (2007) then examined their revised tooth mark frequencies in light of the experimental framework developed by Blumenschine (1995). They found that for size 1 and 2 carcasses, the limb bone mid-shafts are tooth marked at low frequencies (<15% of

NISP) similar to the rates seen in the human followed by carnivore experiments (see Chapter 3 for a discussion of these experiments). For large-sized carcasses, they found long bone mid-shafts were tooth marked slightly less (9.7%) than seen in the human followed by carnivore experiments. Both of these frequencies differed markedly from the carnivore-first models which were tooth marked much more frequently (>70% of NISP). Their study also found slightly lower frequencies of tooth marked epiphyseal and near epiphyseal fragments than in Blumenschine's human followed by carnivore experiments. Additionally, Domínguez-Rodrigo and colleagues argued that the high tooth mark frequencies on metapodials, which Blumenschine interpreted as evidence for initial felid defleshing of carcasses, instead indicate secondary carnivore (mostly likely hyena) scavenging. If felids had initial access to fully fleshed carcasses, they would not likely have tooth marked the metapodials, as these contain almost no nutrition except marrow, which felids cannot access. However, if hominins had first defleshed the carcasses, bone-crunching carnivores may have been attracted to the nutrients remaining in the metapodials. Domínguez-Rodrigo et al. (2007) have interpreted this tooth mark frequency evidence as suggestive of early hominin access at FLK Zinj rather than passive scavenging as had been suggested by Blumenschine.

Blumenschine's group has criticized Domínguez-Rodrigo's claim that they have misidentified biochemical marks as carnivore tooth marks (Blumenschine et al. 2007). They argued that Domínguez-Rodrigo's experiments on biochemical marking were not conducted under strictly controlled conditions and that their results are subjective. Further, they argued that protocols for identifying carnivore tooth marks are well established, and tooth marks are not readily confused with biochemical modifications.

Flesh Availability and the "Hot Zone" Approach

Domínguez-Rodrigo and colleagues also conducted experimental studies of flesh distribution on carcasses surviving felid consumption in order to further test the hypothesis of initial felid access at FLK Zinj (Domínguez-Rodrigo 1999; Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo et al. 2007). They conducted observations of kills made by free ranging lions in the Maasai Mara National Reserve in Kenya and examined the distribution of surviving flesh on carcasses. From this, they developed a "hot/cold zone" scheme, in which hot zones are areas of bone that flesh typically does not survive felid consumption (mainly shaft portions of upper limb elements). Cold zones are then areas where flesh may survive (typically joints and distal limb elements). They posited that cut marks found in hot zones on fossil bones should indicate hominin primary access, as felids would not have left meat in these areas to butcher. When applying this interpretive framework to the FLK Zinj assemblage, Domínguez-Rodrigo et al. found that cut marks often occur in hot zones. They argued that the results of their study refute Blumenschine's three-stage felid-hominin-hyaenid model, and indicate instead that hominins had primary access to fleshed carcasses which were later scavenged by carnivores. Domínguez-Rodrigo and colleagues have argued that the combined evidence of cut marks and carnivore tooth marks suggests early access by hominins, and possibly hunting of smaller mammals.

The work by Domínguez-Rodrigo and colleagues has provided an important contribution to the discussion of Oldowan hominin carcass access. It has highlighted the necessity of bringing multiple lines of evidence into evaluations of site formation processes, including examining patterns as well as frequencies of bone surface modifications. Their "hot zone" approach, for example, does not rely on the frequency of cut marks, which has been shown not to be correlated with butchery intensity (Egeland 2003), but on the anatomical placement of marks in behaviorally informative areas.

Bovid Mortality Profiles

Mortality profiles in an archaeological bone assemblage, or the relative proportion of animals within different age classes (i.e., juvenile, prime adult, old adult), reflect prey selection opportunities available to hominins. These profiles can be viewed within the context of optimal foraging theory, wherein energy expenditure, caloric gain, and risk taken influence foraging decisions (Steele 2003). Bunn and Pickering (2010) have examined bovid mortality profiles at FLK Zinj in order to test predictions arising from the passive scavenging hypothesis, as well as the endurance running / persistence hunting hypothesis. Persistence hunting refers to pursuing prey by either running or walking it to the point of exhaustion. Bramble and Leiberman (2004) suggested that endurance running may have been selected for in early *Homo* approximately 2 Ma as an adaptation for obtaining high quality animal tissues, including meat and marrow. Endurance running may have facilitated hunting by allowing hominins to run mammals to exhaustion. Alternatively, running long distances may have allowed hominins to compete more effectively with other scavengers on the African savannah. Bunn and Pickering (2010) have argued that these hypotheses can be tested by examining bovid mortality profiles (age structure). Mortality profiles in fossil assemblages can be assessed by comparing them to predicted profiles based on modern analogs for differing scenarios of hominin persistence hunting and for hominin scavenging from felid kills. Their predictions are summarized as follows:

1. If hominins were practicing endurance running / persistence hunting to obtain carcasses, bovid mortality profiles should match what cursorial predators (e.g., cheetahs, spotted hyenas) are known to kill (relatively vulnerable young and old) (i.e., an attritional

profile following Klein 1982).

2. If hominins were scavenging size 3 bovids from large felids, bovid mortality profiles should match those of lion kills (an unselective, living-structure prey sample, but with a higher percentage of prime adults than cursorial predators take). As large carnivores typically fully consume small carcasses, scavenging of small (size 1 or 2) carcasses would only have been possible from smaller felids such as leopards or cheetahs. In the case of scavenging smaller carcasses from felids, the bovid mortality profile would be expected to resemble that of leopards (an unselective, living-structure sample).

Bunn and Pickering found that mortality profiles for size 3 bovids at FLK Zinj are dominated by prime-aged adults, and in most cases are inconsistent with test predictions for both persistence hunting and passive scavenging. The "prime dominated" mortality profile was originally defined by Stiner (1990) and is a pattern she argues is associated exclusively with selective hunting by humans of large-sized prey animals (see also Steele 2003). Bunn and Pickering argued that this prime dominated pattern indicates hominins at FLK Zinj may have been ambush predators that obtained larger bovids through hunting.

Aggressive scavenging from lion kills for size 3 bovids is an alternate explanation which Bunn and Pickering did not fully explore. Although leopards take smaller prey, they in fact produce a prey mortality pattern for their size 2 kills not unlike the pattern seen at FLK Zinj for size 3 bovids. As discussed in Chapter 2, there was a greater diversity of large felids in the Early Pleistocene which may have been solitary ambush hunters perhaps more closely resembling modern leopards in behavior than lions (e.g., *Dinofelis*, *Megantereon*). These extinct felids may have provided scavenging opportunities for hominins in woodland environments like FLK Zinj. Taphonomic evidence based on the frequency of carnivore tooth marking and placement of butchery marks on fauna from FLK Zinj reported in this chapter (and by Domínguez-Rodrigo et al. 2007) indicates early access for hominins, which makes passive scavenging unlikely. Aggressive scavenging, however, provides an alternate explanation for the mortality data for large bovids. Mortality profiles for the size 1-2 bovids at FLK Zinj are biased toward older rather than prime individuals, which is a pattern that could indicate persistence hunting.

The debate over the nature of hominin and carnivore activities at FLK Zinj remains unresolved. This is partly due to disagreement over methods of identification and documentation of tooth marks (Domínguez-Rodrigo 2009; Domínguez-Rodrigo and Barba 2006, 2007; Blumenschine et al. 2007). The debate outlined above underscores the need for standardization in identification and data recording methods as well as the need to broaden the comparative sample of Oldowan sites. The study presented here will address these issues through a GIS image analysis of bone preservation and modification patterns at FLK Zinj. As discussed in Chapter 1, GIS allows the comparison of experimental models of carnivore and hominin modification patterns to fossil assemblages in a visual and quantifiable way, and also has the potential to tease apart more subtle patterning which may help to better interpret the competitive interactions of hominins and carnivores at sites. These patterns will be assessed here in light of the GIS analysis of Kanjera South as well as experimental assemblages formed under controlled conditions.

MATERIALS AND METHODS

FLK Zinj Fossil Collection

I collected data on the FLK Zinj specimens during the summer of 2012 at the National Museum of Tanzania in Dar es Salaam. The FLK Zinj archeofauna had recently been repatriated from the National Museums of Kenya, where it had been housed since the Leakey's expeditions. Because of their recent shipment, the FLK Zinj specimens were still packed in their shipping boxes with fossils from other Olduvai sites. I employed two Tanzanian archaeology students to assist me in locating the FLK Zinj fossils in the shipping boxes before beginning data analysis. This process took approximately two weeks. As the museum did not have the space or trays available at the time for storage of the fossils, I repacked them into the boxes after analysis. I created an inventory of the box contents in the process, which I am happy to share with other researchers upon request.

I was able to locate 489 of the original bovid limb specimens from FLK Zinj, and 35 girdle specimens (girdle specimens are not discussed here). These were specimens with a maximum length greater than 2 cm and with good cortical preservation. In comparison, Domínguez-Rodrigo and Barba's (2006) sample had a NISP of 699 long bone fragments, while Blumenschine's (1995) sample included 731 long bone fragments. As my limb sample is smaller, it seems that some of the specimens in these original studies have been misplaced. Hopefully these will be recovered once the collection is completely unpacked. Of the 489 specimens in my study, 292 were identifiable to element and amenable to GIS image analysis (see Chapter 3 Table 3.3).

Identification of Bone Surface Modifications and GIS Image-Analysis

Bone surface modifications were identified and data were collected in the same way as described in the Methods section of Chapter 3. I independently identified all hominin- and carnivore-induced modifications on specimens. I then checked my own identifications against those published by Blumenschine (1995) and Domínguez-Rodrigo et al. (2007).

I conducted GIS analyses following the methodology outlined in Chapter 1 and supplement to Chapter 1. Unlike the Kanjera assemblage, the sample size for tooth marked limb specimens from FLK Zinj was large enough in some cases to perform GIS cluster and density analyses on. I plotted individual tooth marks on GIS element templates following the protocol in Chapter 1. The cluster analysis measures the distance between tooth marks and uses an average nearest neighbor distance statistic to determine if marks are significantly clustered relative to a hypothetical random distribution. I used the GIS Kernel Density tool to visually identify where these clusters occurred on element templates in the figures.

I sorted bones into two groups for all analyses. The small/medium group includes size classes 1-3a, and the large group includes size 3b and above. The size class 1 specimens were separated out in the Kanjera South analysis, but the sample size was too low to analyze the size 1 specimens separately here. Their inclusion with the size 2-3a sample does not affect the pattern of bone preservation, so the size 1-3a sample from FLK Zinj is analytically comparable to the size 2-3a sample from Kanjera. I have included size 3a together with smaller animals in order to make the GIS analyses easily comparable to Kanjera South, which has a majority of bovid specimens on the border between size 2 and 3. This is different from Domínguez-Rodrigo et al.'s (2007) grouping which considers size 1 and 2 animals as small, and size 3 and 4 as large.

RESULTS: BONE PORTION SURVIVORSHIP AT FLK ZINJ

This section presents results of GIS analyses of bone portion survivorship. These patterns are fully illustrated in Figures 4.1-4.4, and are compared with GIS analyses of experimental models of bone damage described in Chapter 3 and fully illustrated in Appendix A. These comparative GIS models are based on Blumenschine's hammerstone, hammerstone-to-carnivore, and carnivore only (hyaenid) experiments, as well as my own carnivore experiments presented in Chapters 1 and 2.

Bone Portion Survivorship – FLK Zinj Small and Medium Bovids

Hindlimb

Small and medium-sized femora at FLK Zinj are well-preserved, but fragmented in a pattern resembling the hammerstone damaged experimental models (Fig. 4.1, Appendix Fig. A.2). From the pattern of preservation observed in this element, it is clear that carnivores or other density mediated agents did not completely remove the epiphyses.

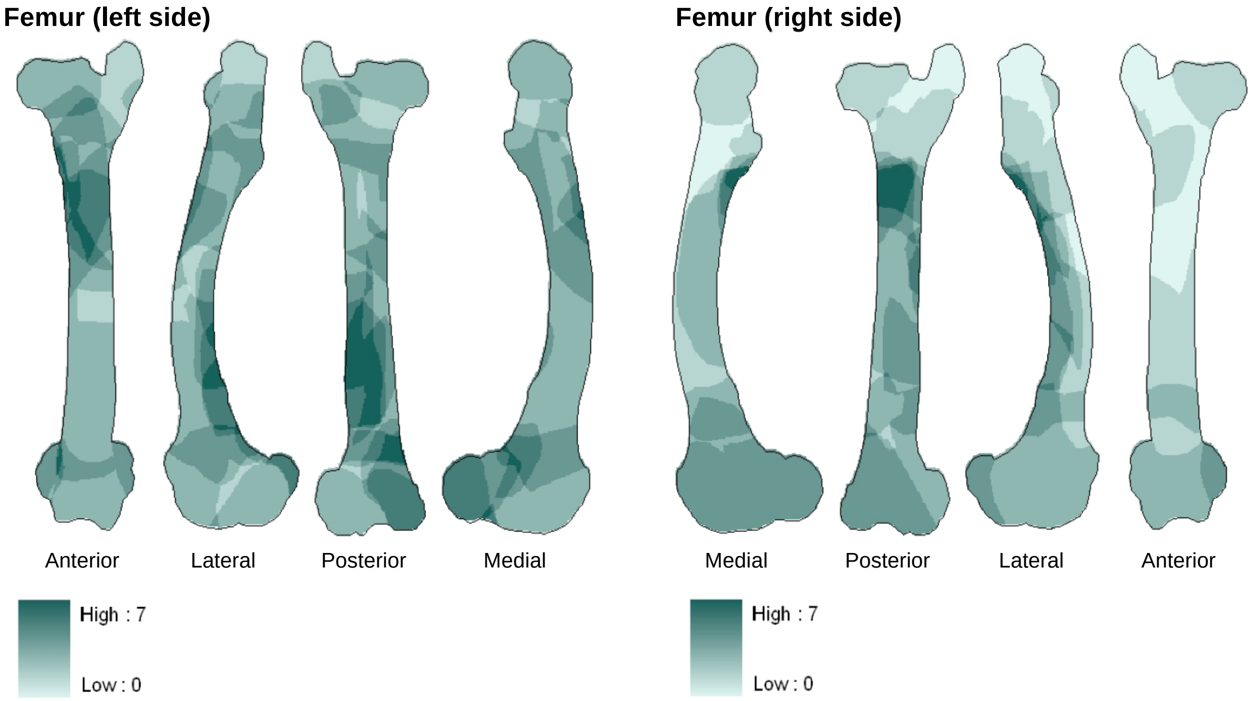
The small and medium-sized tibiae at FLK Zinj show a similar pattern of relatively even preservation across bone regions. The highest preservation is seen in the midshafts, some proximal epiphyses are deleted, but distal epiphyses are relatively well preserved. This pattern is also similar to preservation seen in the tibiae at Kanjera South (Fig. 4.1, Appendix Fig. A.3).

The pattern of preservation in the metatarsals at FLK Zinj is slightly different between the left and right sides (Fig. 4.1). Both sides are highly fragmented, as seen in the hammerstone only models, but the lower preservation of distal epiphyses may reflect a slightly higher level of attrition due to carnivore activity. Both right and left metatarsals are highly fragmented, but the right side is missing more distal epiphyses. This slight variation is not unexpected given the relatively small samples sizes. The pattern on the metatarsals overall is most consistent with the hammerstone only model, while the hammerstone-to-carnivore model is too small to make an informed comparison. (Appendix Fig. A.6).

Forelimb

The pattern seen in the humeri at FLK Zinj (Fig. 4.2) is similar to the pattern at Kanjera South (Appendix Fig. A.7). Ulnae are typically highly fragmented, similar to the hammerstone

Figure 4.1. Preservation of small and medium bovid hindlimbs at FLK Zinj. (size class 1-3a). High = minimum number of elements estimate (greatest number of overlapping fragments).



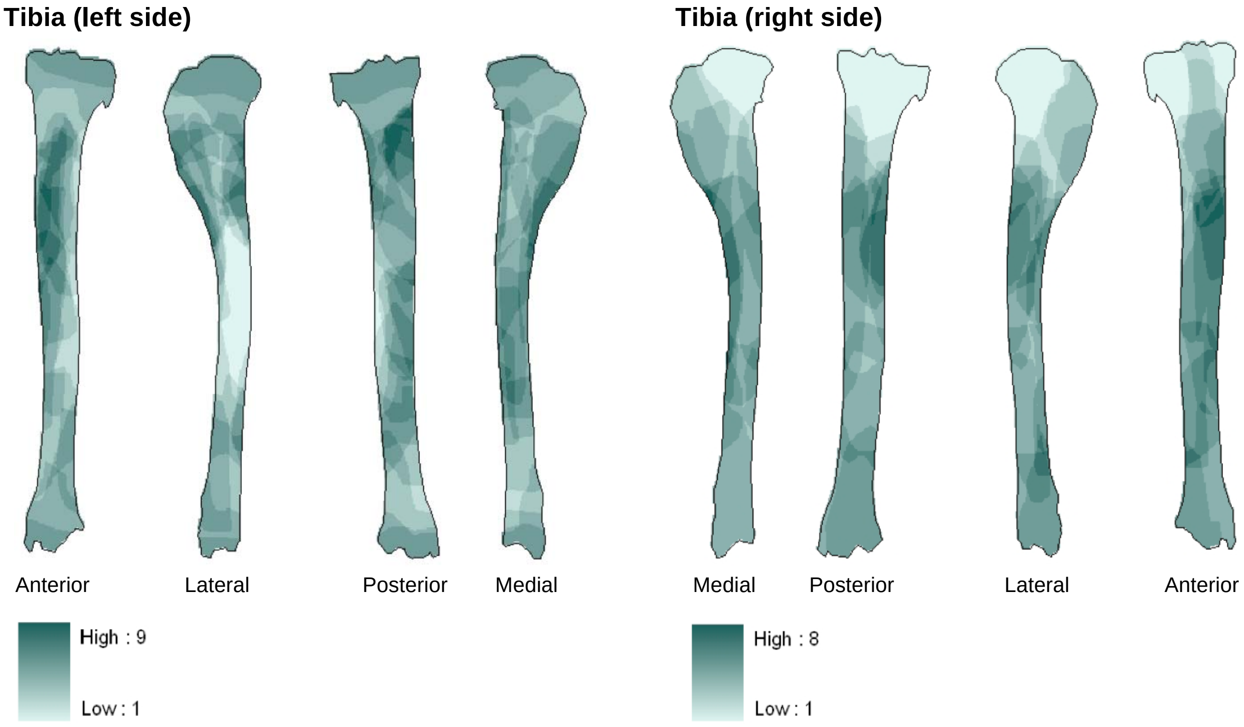
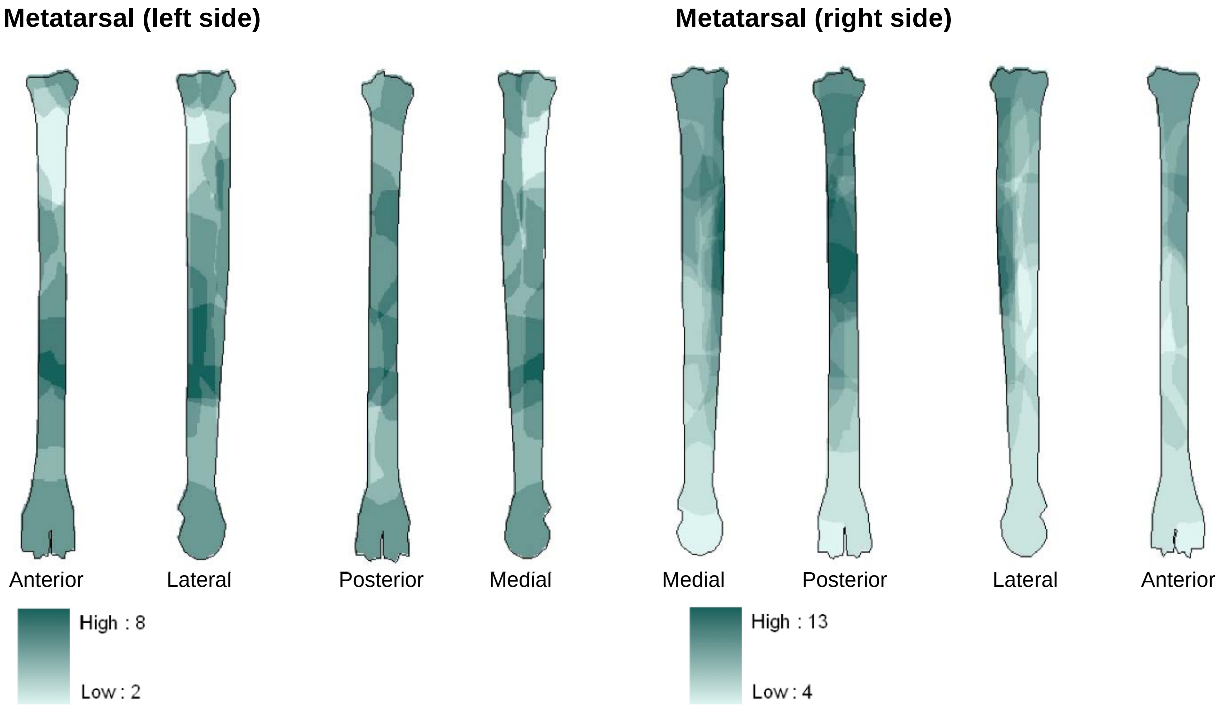


Figure 4.1 continued

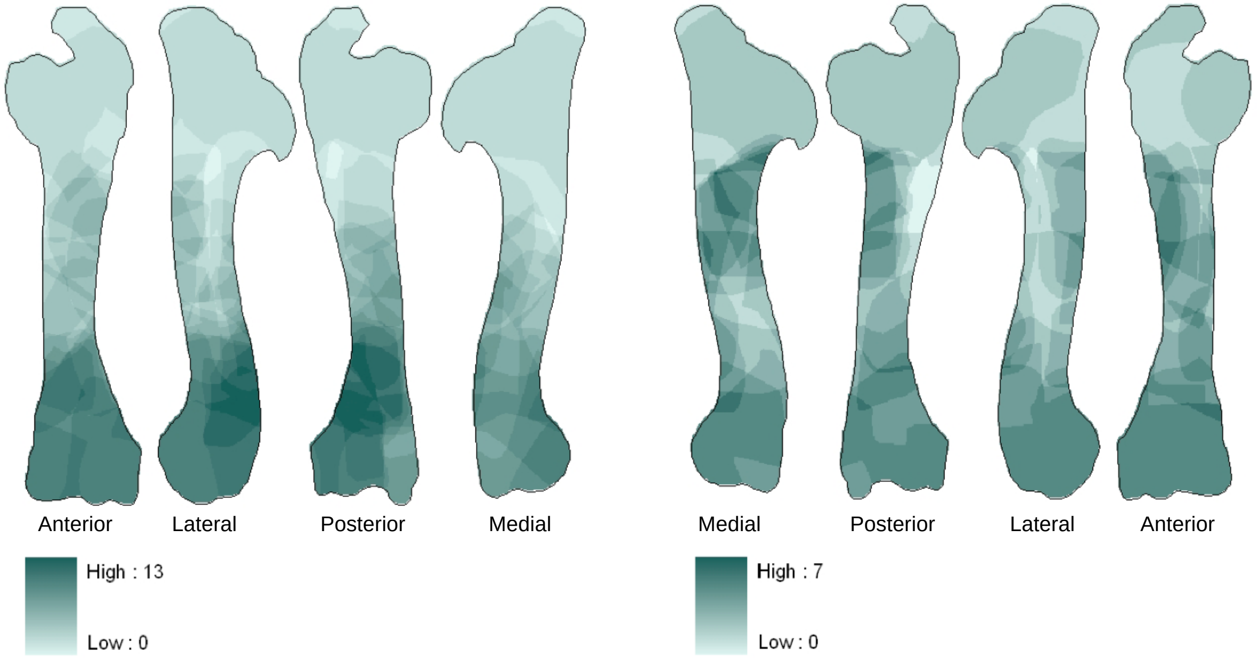


experimental models (Appendix Fig. A.8), but do not display the same degree of epiphyseal deletion seen in the hammerstone-to-carnivore experiments.

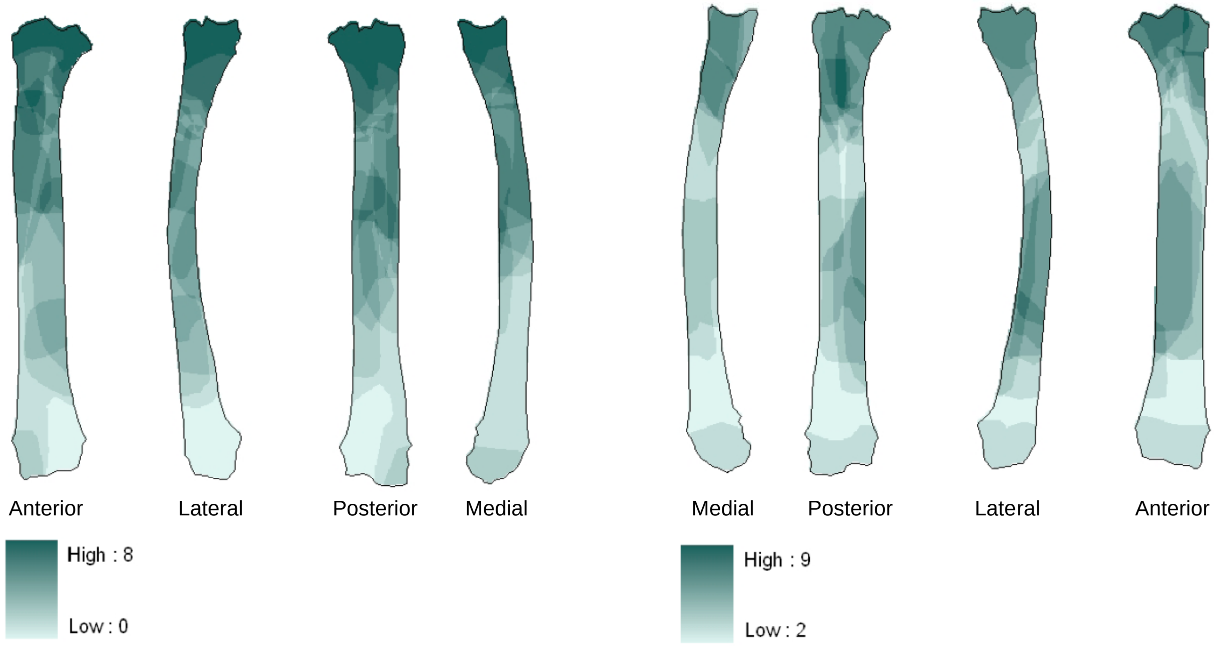
The radii at FLK Zinj show greater preservation at the proximal end and shaft than at the distal end. Concordantly, the proximal ulnae are often well preserved, with intact olecranon processes. This pattern differs somewhat from Kanjera, where distal radial epiphyses are preserved at frequencies approaching the proximal epiphyses in size 2 to 3a bovids, and the olecranon processes are generally missing from proximal ulnae.

The majority of metacarpals at FLK Zinj show a similar pattern of preservation to that at Kanjera and exhibit a pattern consistent with the hammerstone only experimental models (Fig. 4.2, Appendix Figs. A.13-A.14).

Figure 4.2. Preservation of small and medium bovid forelimbs at FLK Zinj. (size class 1-3a). High = minimum number of elements estimate (greatest number of overlapping fragments.

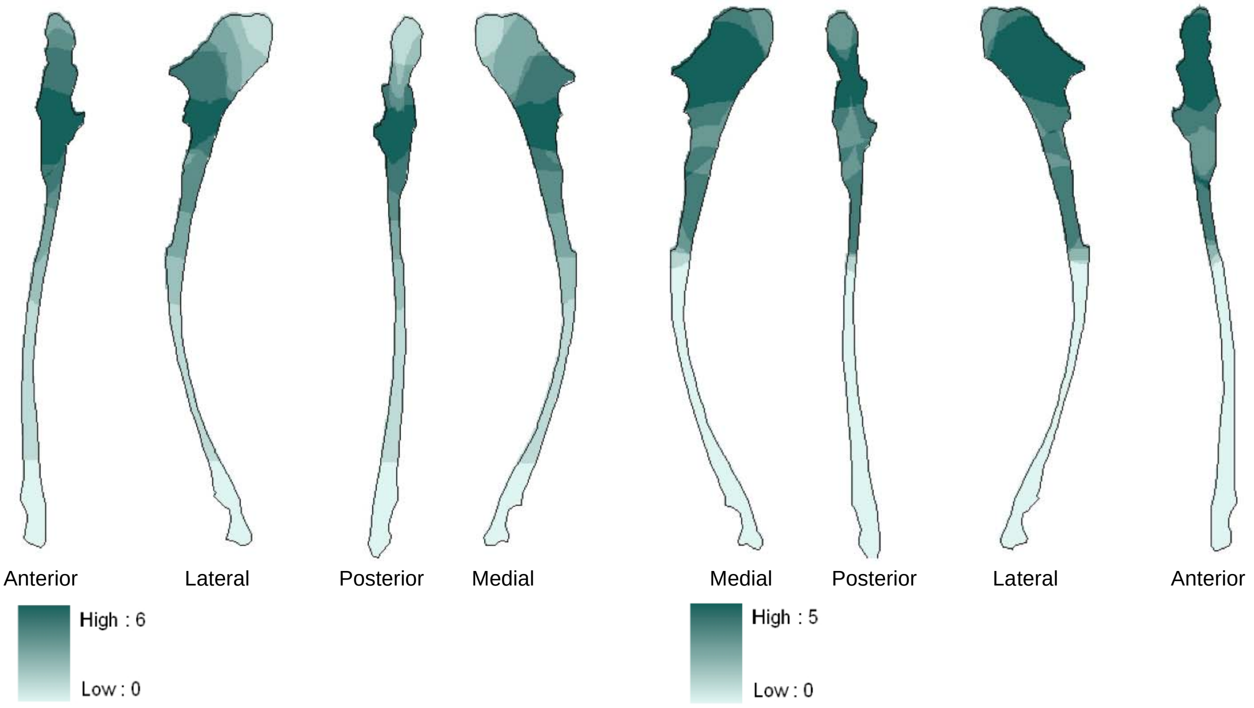

Humerus (left side)

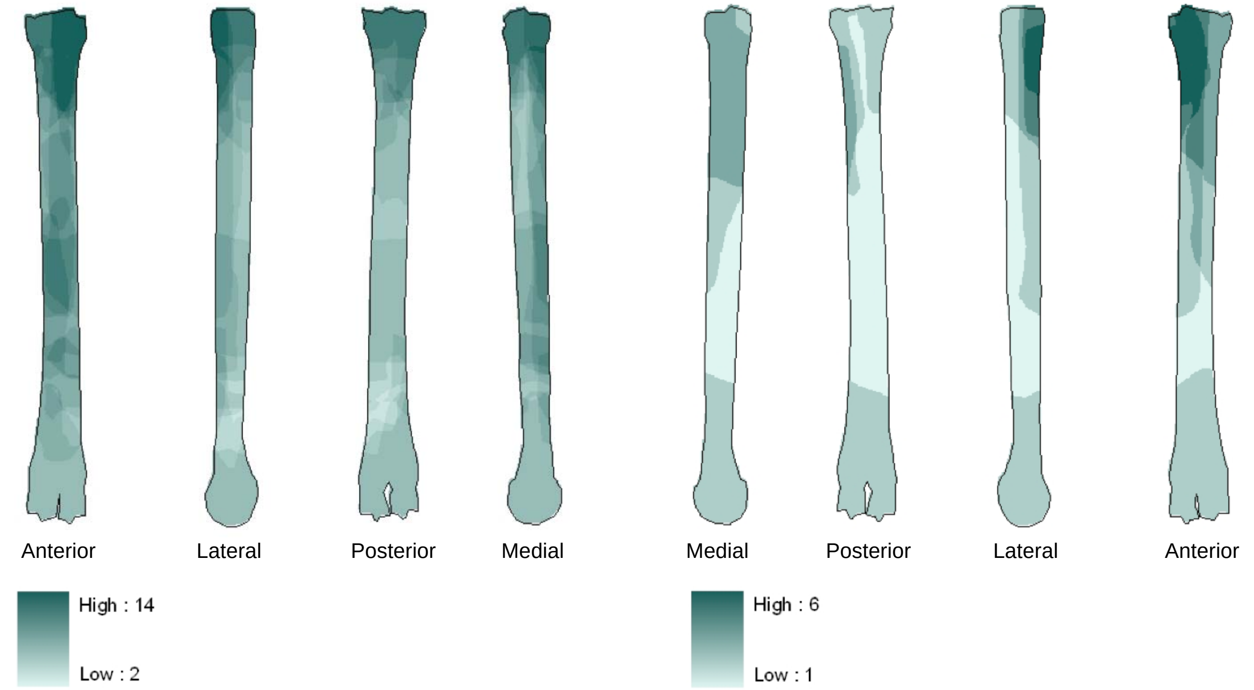
Humerus (right side)


Radius (left side)

Radius (right side)

Figure 4.1 continued


Ulna (left side) **Ulna (right side)**


Metacarpal (left side) **Metacarpal (right side)**

Bone Portion Survivorship – FLK Zinj Large Bovids

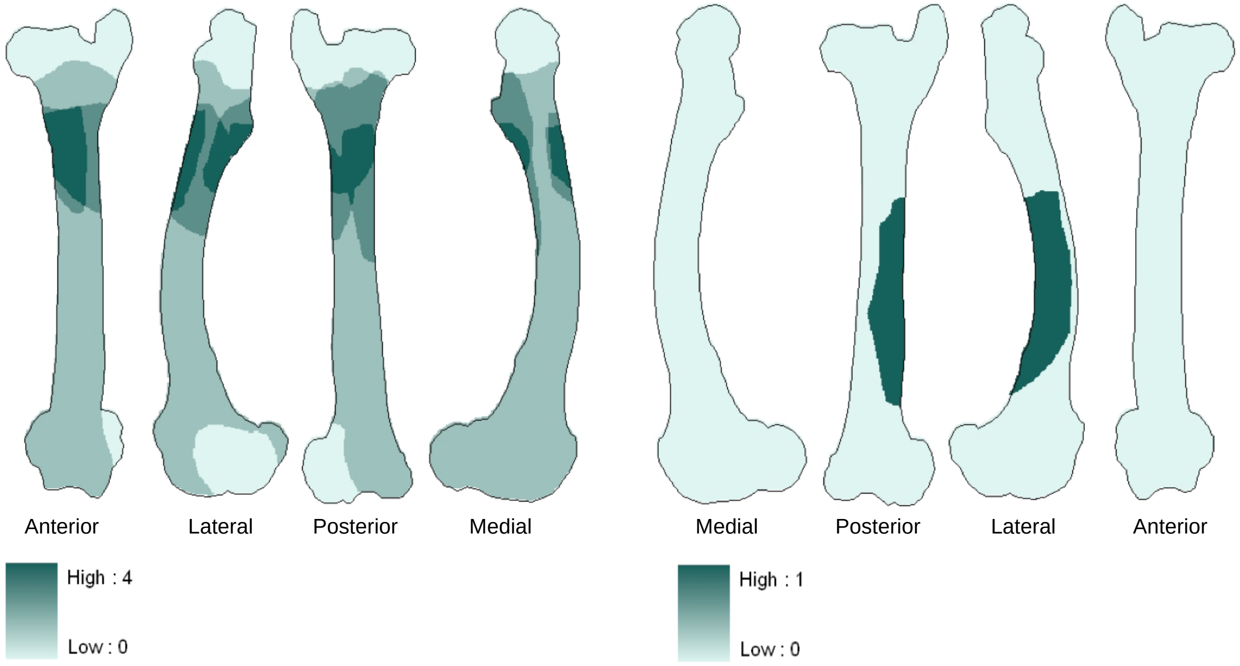
Hindlimb

The large, size 3b femora are highly fragmented at FLK Zinj (Fig. 4.3). The majority of fragments preserved are shaft fragments, while epiphyses are generally not preserved. The size 3b sample from FLK Zinj included in the GIS analysis is poorly represented in comparison to the sample from smaller bovids, so the better regional representation of fragments across the femora for smaller bovids may be related to sample size. The pattern is consistent with what is seen in the large femora at Kanjera (Appendix Fig. A.15). It is difficult to compare to experimental models due to small sample sizes for models, but the fragmentation level is suggestive of hammerstone breakage. This is further supported by the presence of percussion notches on the large femora and absence of intensive carnivore tooth marking.

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

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

Figure 4.3. Preservation of large bovid hindlimbs at FLK Zinj. (size class 3b-4). High = minimum number of elements estimate (greatest number of overlapping fragments.


Femur (left side) **Femur (right side)**

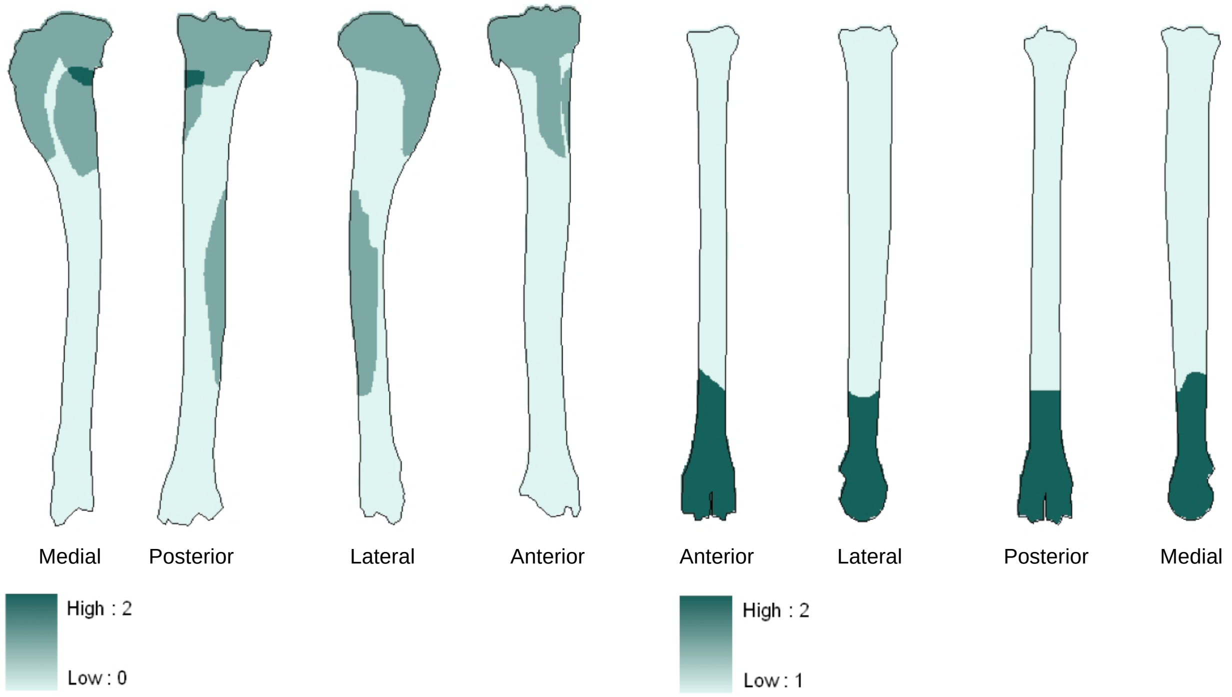
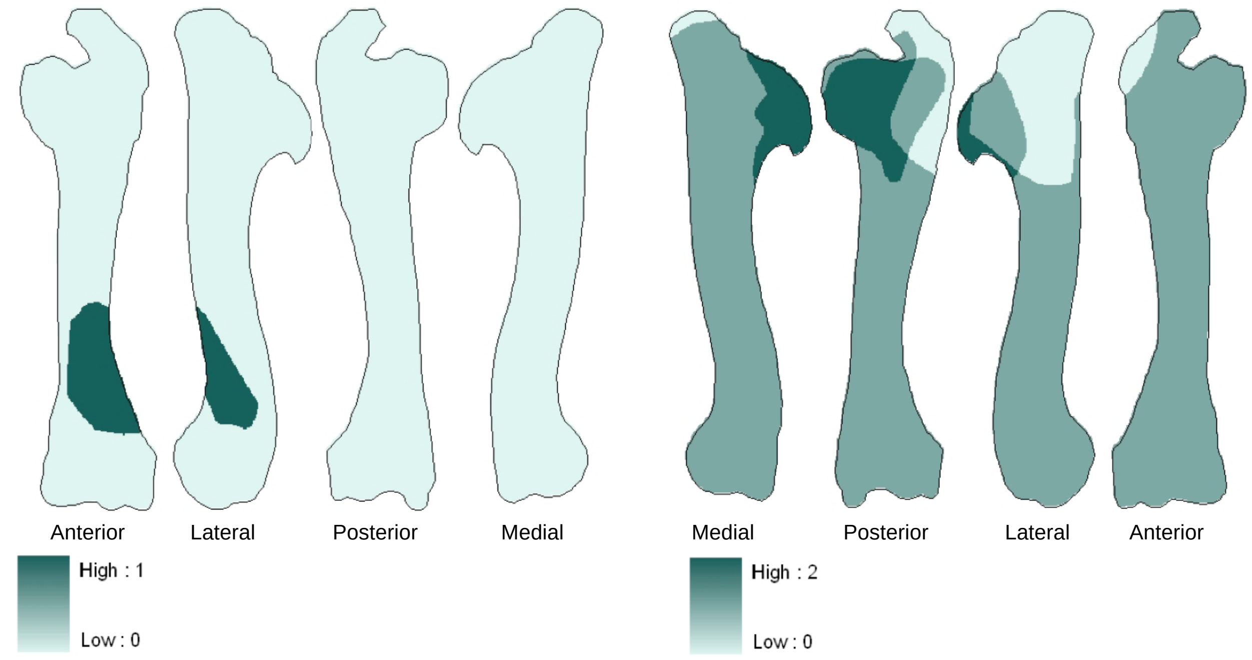
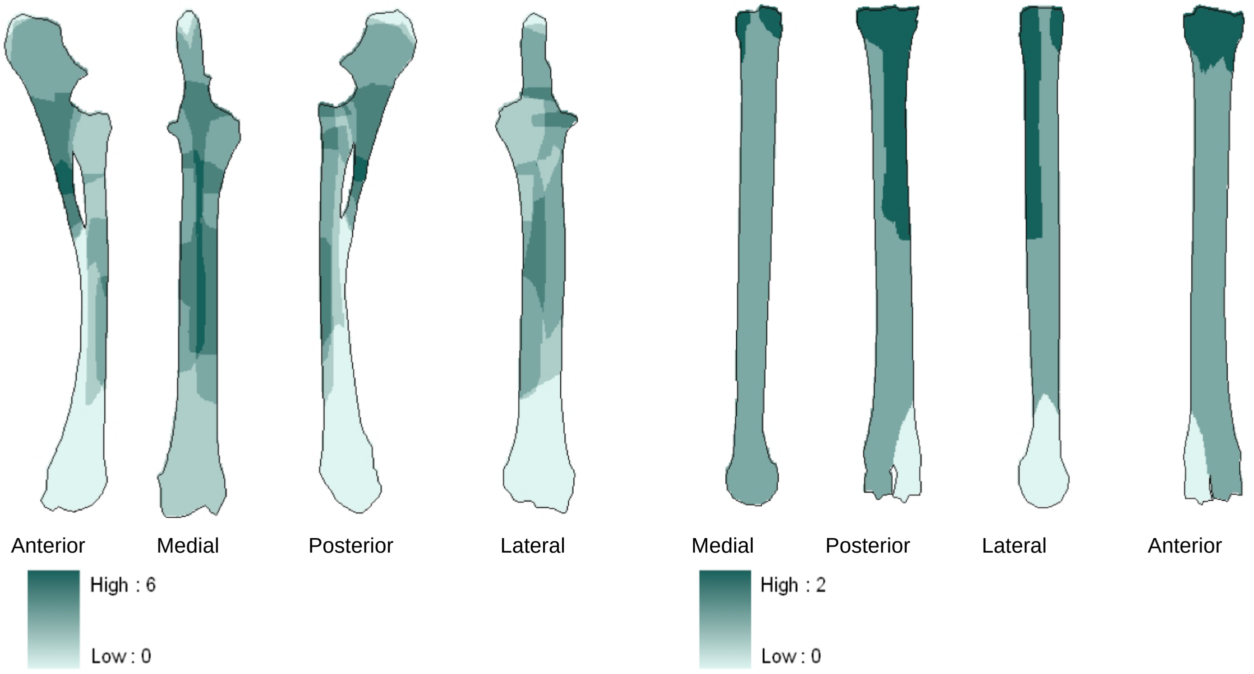

Tibia (right side) (no left side) **Metatarsal (left side)** (no right side)

Figure 4.4. Preservation of large bovid forelimbs at FLK Zinj. (size class 3b-4). High = minimum number of elements estimate (greatest number of overlapping fragments.

Humerus (left side) **Humerus (right side)**



Radio-Ulna (right side) **Metacarpal (right side)**



Forelimb

Preservation of the proximal epiphysis in large humeri is consistent with experimental models with little or no carnivore involvement, as this portion is often consumed by carnivores due to its low density and high grease content (Fig. 4.4, Appendix Fig. A.15).

The large radio-ulnae from Zinj show preservation of the midshaft and olecranon process and deletion of the distal end. This is a pattern most consistent with the hammerstone-to-carnivore experimental model (Appendix Fig. A.19).

Of the two metacarpal specimens I was able to place on the GIS template, one was mostly complete, and the other was a proximal fragment. Although the sample size is small, the pattern of metacarpal preservation at FLK Zinj is most similar to the hammerstone-to-carnivore experimental model (Appendix Fig. A.20).

RESULTS: BONE MODIFICATION PATTERNS

This section presents results of GIS analyses of the distribution of various types of hominin- and carnivore-induced damage to bones from FLK Zinj. I consider small (size 1-3a) and large (size 3b and above) specimens separately. See Materials and Methods section for a further description of size class breakdowns. Analyses are fully illustrated in Figures 4.5-4.8. I present GIS density and cluster analyses to determine whether marks occur in significant clusters. Density and cluster analyses are presented when sample sizes are large enough (more than 5 modifications in a particular view – e.g., more than 5 tooth marks on the anterior femur). Where sample sizes are not large enough to conduct statistical analyses, I display plots of individual marks on element templates instead.

It should be noted that the distribution of cut and tooth marking at FLK Zinj has been previously documented by Domínguez-Rodrigo et al. (2007) and Domínguez-Rodrigo and Barba (2006). While my identifications of these modifications are mostly consistent with theirs, my plots of the anatomical distribution of cut marks and tooth marks are slightly different. This is because in order to make my diagrams easily comparable with Kanjera South, which has a majority of bovid specimens on the border between size class 2 and 3a, I have included size 3a specimens from FLK Zinj on the small template. Domínguez-Rodrigo's groupings are broken into small (size 1-2) and large (size 3a and above).

Patterns of Carnivore Damage – Small and Medium Bovids

Hindlimb

Although carnivore tooth marking is reported to occur on small bovid femora from FLK Zinj at a frequency of about 14% (on both shaft and end fragments) by Domínguez-Rodrigo and Barba (2006) (see Chapter 2 Fig. 2.3), specimens bearing tooth marks were not amenable to GIS image analysis. For the tibiae, GIS cluster analyses show a random pattern of tooth mark distribution on the anterior, lateral, and posterior aspects, but a significant ($p = <0.001$) cluster proximally on the postero-medial aspect of the shaft and on the medial aspect of the midshaft (Table 4.1). Metatarsals do not show significant clustering of tooth marks, but are more heavily gnawed at the distal end.

Forelimb

The small and medium sized humeri from FLK Zinj (Fig. 4.5) show significantly dense clusters of tooth marks distally on the anterior shaft and trochlea as well as on the on the lateral shaft. Tooth marking on the trochlea is similar to what is seen at Kanjera and in the carnivore

Table 4.1. GIS Cluster Analysis for tooth marks on small and medium bovid limb elements from FLK Zinj. Analysis was performed on four aspects of all elements. The distance between each tooth pit and its nearest neighbor was measured. The nearest neighbor index (NNI) is the observed distance divided by the average expected distance in a hypothetical random distribution. If the NNI is less than 1, the pattern is considered clustered. If the NNI is greater than 1, the trend is toward dispersion. P-values indicating significant clustering of tooth pits appear in bold. Cells with n/a indicate sample sizes too small for analysis (containing less than 5 individual tooth marks).

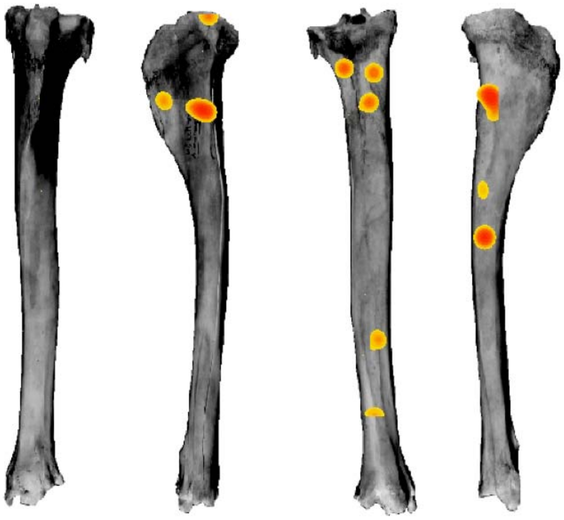
Element	Anterior	Lateral	Posterior	Medial
Humerus	Clustered	Clustered	Random	Random
NNI	0.54	0.28	0.73	0.72
p	**0.01**	**0.002**	0.15	0.16
Radius	n/a	n/a	Random	n/a
NNI			0.75	
p			0.247	
Ulna	n/a	n/a	n/a	Random
NNI				1.08
p				0.714
Metacarpal	Dispersed	n/a	Clustered	Clustered
NNI	1.55		0.40	0.62
p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

only experimental models. However, the hammerstone-to-carnivore model consists of only 3 specimens, and thus may not be an accurate model of carnivore secondary access (Appendix Fig. B.4).

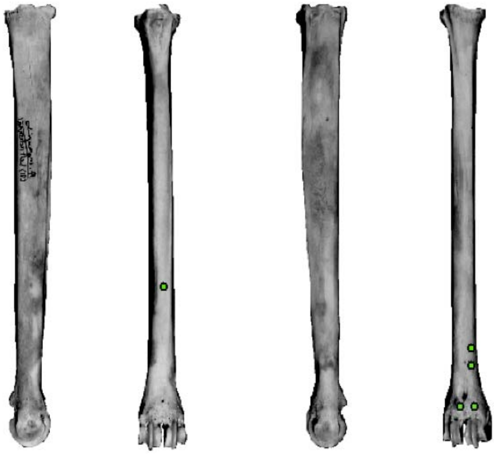
The radii and ulnae are both tooth marked, but where sample sizes are large enough to perform cluster analyses, results show tooth marks are randomly distributed. The pattern of tooth marking on the radio-ulnae at FLK Zinj differ from what is seen at Kanjera and in the carnivore only experimental model, in that tooth marks are not confined to the olecranon on the ulna in the FLK Zinj specimens (Appendix Fig. B.6). A hammerstone-to-carnivore experimental model is not available for the radius or ulna.

Figure 4.5. Distribution of carnivore damage on the small and medium bovids from FLK Zinj. Figures represent composites of modifications on right and left elements shown on a left side template. Where sample sizes are large enough and clustering is significant, GIS density analyses are shown. Where sample sizes are small, distribution of individual tooth marks is shown. Tooth marking includes both pits and scores. n = the number of specimens bearing tooth marks.

Femur n/a



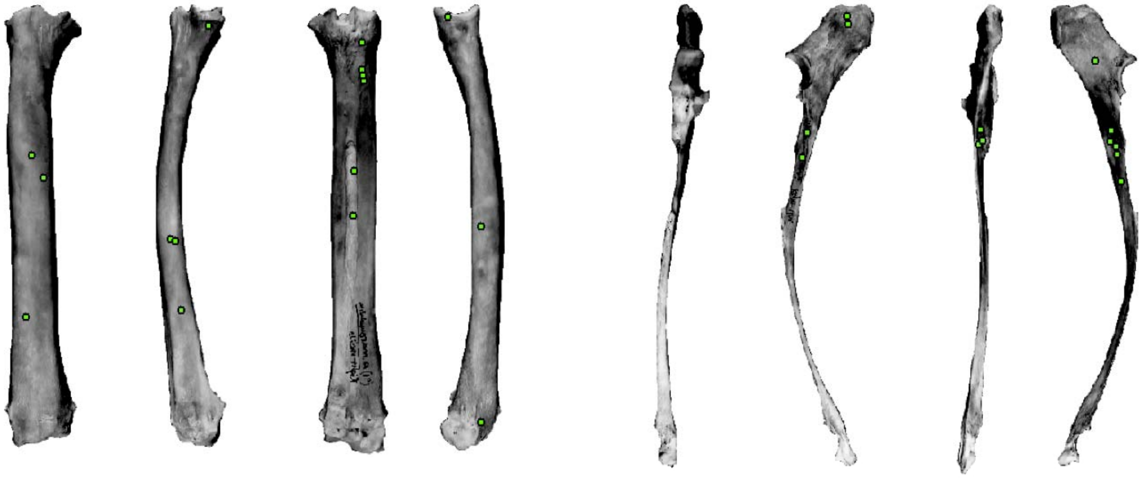
Tibia n=20



Metatarsals n=5

Humerus n=13

Figure 4.5 continued



Radius n=13

Ulna n=3

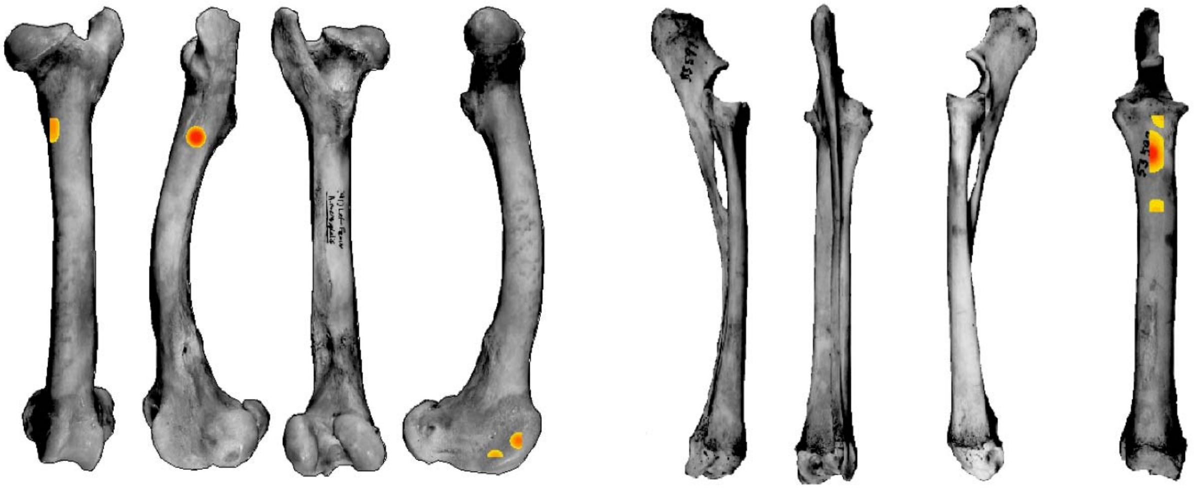
Metacarpal n=8

Finally, the metacarpals show significant clusters of tooth marks on the posterior shaft proximally and distally, as well as on the proximal-medial shaft. These clusters also occur in the carnivore only experimental model. The hammerstone-to-carnivore experimental model shows a similar tooth mark cluster on the medial shaft, however, the sample size is only one for this model, and so other potential areas of clustering may not have been preserved (Appendix Fig. B.7).

Patterns of Carnivore Damage – Large Bovids

Only the large bovid femora and radio-ulnae from FLK Zinj were complete enough to be amenable to GIS analysis. Femora show significant clustering of tooth marks on the lateral shaft at the proximal end as well as on the medial distal condyle (Table 4.2, Fig. 4.6). Tooth marks are not clustered in these areas in either of the experimental carnivore modified assemblages (Appendix Fig. B.9). The radius displays tooth mark clustering on the proximal end of the anterior shaft. A non-significant cluster of tooth marks appears in this same area in the single Kanjera large bovid radius preserved (Fig. 3.9). The carnivore only experiments do not show a cluster in this area, and a hammerstone-to-carnivore experimental model is not available. This similarity in patterning between FLK Zinj and Kanjera may indicate the involvement of a similar kind of carnivore, but without a larger sample size no definitive interpretations can be made.

Figure 4.6. Distribution of carnivore damage on the large bovids from FLK Zinj. Figures represent composites of modifications on right and left elements shown on a left side template. Only samples for the femur and radio-ulna were available, but these were large enough to conduct density analyses, which are shown here. Tooth marking includes both pits and scores. n = the number of specimens bearing tooth marks.



Femur n=1

Radio-Ulna n=6

Table 4.2. GIS Cluster Analysis for tooth marks on large bovid limb elements from FLK Zinj.

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

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

Patterns of Hominin Damage – Small and Medium Bovids

Cut marks occur in all limb element categories in small and medium bovids from FLK Zinj. However, of these elements, only the humerus and radius had high enough modification counts to perform cluster analyses on. Results show these patterns are either random or dispersed, and marks are not clustered in any particular area (Table 4.3).

Table 4.3. GIS Cluster Analysis for cut marks on small and medium limb elements from FLK Zinj. Analysis was performed on four aspects of the humerus and radius, as sample sizes for other limb elements were too low (<5 cut marks per aspect). The distance between each mark and its nearest neighbor was measured. The nearest neighbor index (NNI) is the observed distance divided by the average expected distance in a hypothetical random distribution. If the NNI is less than 1, the pattern is considered clustered. If the NNI is greater than 1, the trend is toward dispersion. Empty cells indicate sample sizes too small for analysis (containing less than 5 individual cut marks). No elements showed significant clusters of cut marks.

Element	Anterior	Lateral	Posterior	Medial
Humerus	Random	Dispersed	Dispersed	Random
NNI	1.15	1.15	1.16	1.16
p	0.12	0.14	0.11	0.11
Radius	Random	n/a	n/a	n/a
NNI	1.05			
p	0.740			

Domínguez-Rodrigo et al. (2006) analyzed the distribution of cut marks and found them in hot zones on all upper and intermediate limb elements. Cut marking occurs in hot zones most frequently in the radii and humeri, and less frequently in the femora and tibiae. The distribution of these marks in hot zones is similar to what they found in experiments with fully fleshed carcasses. Domínguez-Rodrigo and colleagues (2006) have argued that this reflects hominin early access to fleshed carcasses, prior to carnivore involvement.

Hindlimb

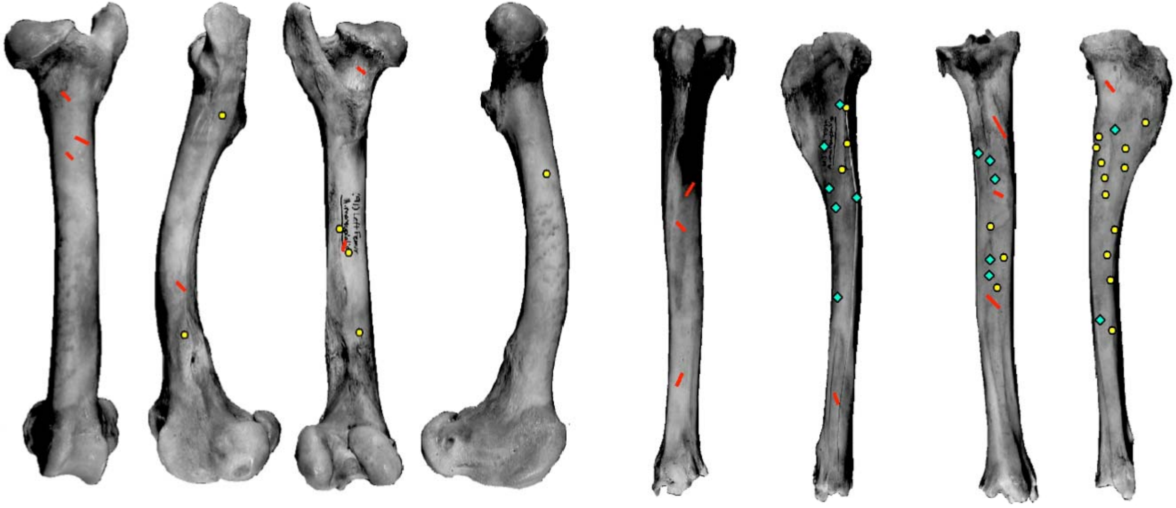
In terms of the location of hominin-induced modifications on the FLK Zinj bones relative to experimental models, the femora from FLK Zinj do not bear the disarticulation marks at the distal epiphysis present in the hammerstone only experimental models (Fig. 4.7, Appendix Fig. B.10). Yet, the femora do bear some percussion marks. The tibiae preserve cut marks across the shaft, and intensive percussion marking including notches on the posterior, medial, and lateral aspects. This pattern is somewhat similar to what is found at Kanjera (Appendix Fig. B.11), but more intensive.

Metatarsals from FLK Zinj bear some cut marking at the distal end, but are heavily percussion marked (more so than at Kanjera), indicating thorough demarrowing by hominins of these lower limb elements.

Forelimb

Hominin-induced modifications on the FLK Zinj humeri are confined to the shaft, but are not clustered in any particular area. The presence of these modifications certainly indicates flesh removal and hammerstone breakage, but the pattern does not resemble either the hammerstone only or hammerstone-to-carnivore experimental models (Appendix Fig. B.13). The hammerstone only model shows cut marks mainly on the epiphyses and metaphyses, not the midshafts, while the hammerstone-to-carnivore models show cutmarks on the shafts. However,

Figure 4.7. Distribution of cut and percussion marking on the small and medium bovids from FLK Zinj. Figures represent composites of modifications on right and left elements shown on a left side template. n = the number of specimens bearing marks.



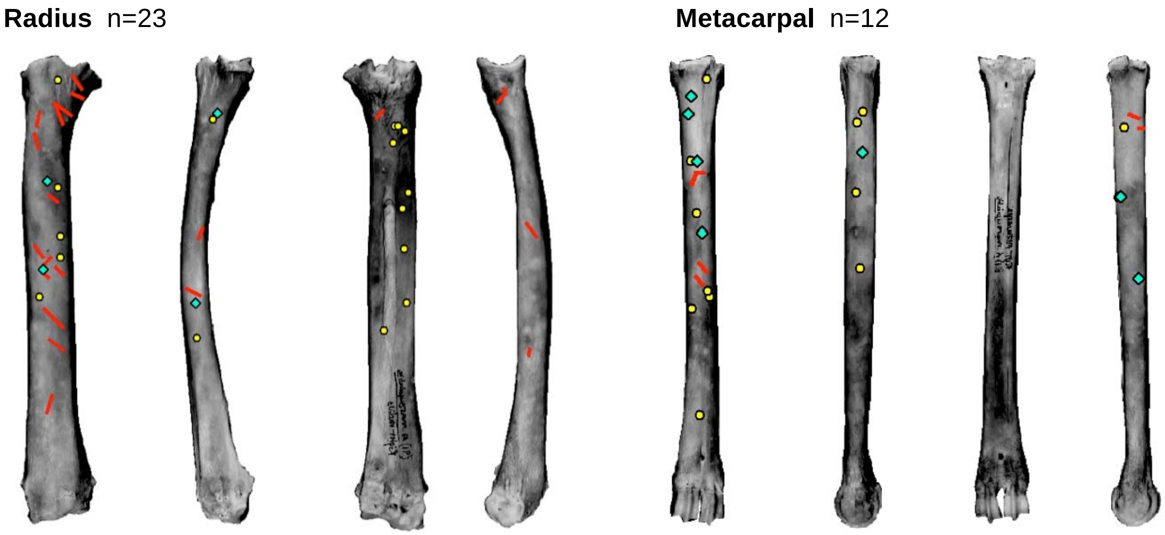
Femur n=7

Tibia n=18

Metatarsal n=19

Humerus n=25

Figure 4.7 continued



the sample size is very small for the hammerstone-to-carnivore model making it difficult to confidently use for comparison.

Radii from FLK Zinj are heavily modified, but cut marks are not clustered in any particular area (Fig. 4.7). Hominin processing of the FLK Zinj radii is more intensive than at Kanjera, although not as intensive as is seen in the experimental models. Percussion marking is heaviest on the posterior aspect of the radii at FLK Zinj, which is also seen in the hammerstone only model, however, the model also shows heavy percussion damage laterally, which is not seen at FLK Zinj (Appendix Fig. B.15). The hominins at FLK Zinj were probably resting the flat posterior surface of the radius against an anvil and striking the anterior surface to break open the bone. There are no small or medium hominin-modified ulnae included in the GIS analysis.

Finally, small and medium metacarpals are heavily modified at FLK Zinj in the same way as the metatarsals, except that metacarpals have cut marked shafts. Cut marks probably reflect tendon removal, while the percussion marks were generated during demarrowing.

Patterns of Hominin Damage – Large Bovids

For the larger (size 3b) bovids at FLK Zinj, only the femur, humerus and radio-ulna were available for GIS analysis. Oliver (1994) found a cut mark frequency of 15% for large femora, but I was unable to place these marks on the GIS template. Figure 4.8 displays the location of percussion notches on the large femora. Experimental models of human damage are unavailable for large femora.

Figure 4.8. Distribution of cut and percussion marking on the large bovids from FLK Zinj. Figures represent composites of modifications on right and left elements shown on a left side template. n = the number of specimens bearing marks.

Femur n=1

Humerus n=1

Radio-Ulna n=4

One cut mark occurs on a large bovid humerus at FLK Zinj located just under the humeral head (Fig. 4.8). This mark is in Domínguez-Rodrigo's cold zone, and so is uninformative regarding priority of access. The large radio-ulnae, however, are more heavily cut marked. The distribution of these marks is random, but nearly all occur in hot zones, clearly demonstrating removal of tissue by hominins. In comparison, the large radio-ulnae from Kanjera do not display cut marks in hot zones.

BONE MODIFICATION FREQUENCIES AT FLK ZINJ

Bone modification frequencies at FLK Zinj have been discussed and debated at length in the literature (Oliver 1994; Blumenschine 1995; Capaldo 1997; Domínguez-Rodrigo 1997; Selvaggio 1998; Domínguez-Rodrigo and Pickering 2003; Domínguez-Rodrigo and Barba 2006; Blumenschine et al. 2007; Domínguez-Rodrigo et al. 2007; Pante et al. 2012). This debate is detailed in the Background section above. Due to differences in methodology and disagreement over identifications of bone surface modifications (especially tooth marks), there is currently no consensus on bone surface modification frequencies in the FLK Zinj assemblage. I calculated bone modification frequencies independently in the sample I used in the GIS analysis, and I then compared each specimen against those identified as damaged by Blumenschine (1995) and Domínguez-Rodrigo et al. (2007). Percent agreement of my bone surface modification frequencies with these previous studies is reported in Table 4.4.

Percussion Mark and Tooth Mark Frequencies

Of the 489 specimens examined in both this study and in Domínguez-Rodrigo's, I identified approximately 23% as percussion marked, while Domínguez-Rodrigo identified approximately 24% (note this differs slightly from Domínguez-Rodrigo's published frequency as

I consider here only the sample we analyzed in common). For the sample this study shared in common with Blumenschine's study, I found a percussion mark frequency of 30%, while Blumenschine identified 40% of these as percussion marked. Blumenschine did not study cut marks, but 87% of the cut marked specimens identified in this study (16% of the total sample), were also identified as cut marked by Domínguez-Rodrigo.

Table 4.4. Comparison of bone surface modifications on limb specimens in this study compared with those identified by Domínguez-Rodrigo et al. (2007) and Blumenschine (1995)

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

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

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

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

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

Biochemical/Bioerosion Damage

Domínguez-Rodrigo and Barba (2006) argue that some modifications originally identified as tooth marks by Blumenschine were instead equifinalities produced by biochemical processes. They cite experimental studies of fungal damage to bone showing that biochemical processes / bioerosion can superficially mimic tooth marking. They argued that misidentification of biochemical marks as tooth marks was the cause of the higher tooth mark frequencies in Blumenschine's original analysis compared to their own.

These differing interpretations of tooth mark frequencies between researchers have implications for understanding site function at FLK Zinj. High frequencies of tooth marking have been used by Blumenschine and colleagues to support a three-stage model of secondary access by hominins to felid kills and subsequent scavenging by hyenas of hominin food refuse. This model, they argued, best incorporates the evidence of hammerstone breakage of long bones by hominins as well as the high frequency of carnivore tooth marking. Domínguez-Rodrigo and colleagues have argued that their lower, revised tooth mark frequencies instead support early access to fleshed carcasses, and possibly hunting by hominins.

Blumenschine et al. (2007) have countered Domínguez-Rodrigo et al.'s revised tooth mark frequency estimate, arguing that it is unsupported. They argued that tooth pits and scores are not easily confused with bioerosion. Pits and scores are typically much larger in size than bioerosion markings, and anatomical patterning of bioerosion does not resemble patterning of tooth marking. For example, bioerosion channels typically form an interconnected, meandering pattern whereas tooth marks do not. Also, Blumenschine and colleagues argued that the internal morphology of biochemical marks is smooth, unlike the internal crushing that characterizes tooth pits. Further, biochemical marks may be composed of a cluster of "micro-pits" which is not characteristic of carnivore tooth marking. Blumenschine and colleagues also criticized Domínguez-Rodrigo et al. for providng a qualitative description of bioerosion based on a small study without control samples. These arguments make clear the hazards potential equifinality can pose for assemblage analysis and interpretation.

In my own analysis of the FLK Zinj assemblage, I observed biochemical damage as defined by Domínguez-Rodrigo and Barba (Fig. 4.9), and in many cases it does superficially resemble carnivore tooth marks. I did not conduct a thorough, quantitative examination of biochemical damage in the FLK Zinj assemblage, but I did frequently observe its presence in the collection. I also observed staining on some bone surfaces likely attributable to root etching (which was also identified by Blumenschine). Biochemical damage could potentially have been a factor in the higher tooth mark frequencies reported by Blumenschine.

Figure 4.9. Examples of Biochemical Marking in Specimens from FLK Zinj. The image on the left (Cat.# A22) was also identified by Dominguez-Rodrigo (2007, Fig. 11d) as displaying biochemical marking. This specimen was <u>not</u> identified in Blumenschine's (1995) study as tooth marked. The image on the right (Cat.# B4-8 (84)) shows more extensive biochemical damage with intersecting scores, irregular in width. This catalog number is duplicated for several different specimens, so it is not possible to tell whether it was identified as tooth marked in previous studies. Scale is the same for both images. Scale bar is 1cm.

DISCUSSION

Extent of Hominin Involvement at FLK Zinj

According to this GIS analysis, the FLK Zinj small- and medium-sized bovids display an overall pattern of cut marks and percussion marks similar to the pattern in the Kanjera assemblage. This is the case for both the hindlimbs and the forelimbs. These two assemblages differ, however, in the frequency with which cut and percussion marks occur, with higher frequencies occurring in the FLK Zinj assemblage. The FLK Zinj pattern does not match the patterns documented in the hammerstone only or hammerstone-to-carnivore experimental models based on Blumenschine's experiments. However, one similarity the FLK Zinj pattern does share with the hammerstone-to-carnivore models is the lack of disarticulation marks on the epiphyses (particularly on the femur and humerus). The distribution of cut marks in the FLK

Zinj assemblage is similar to that of the experimental butchery models based on Plummer's collection, with the majority of cut marks falling within the GIS clustering zones identified in Plummer's experiments. The experiments conducted by Plummer had a significantly larger sample size of femora and tibiae than Blumenschine's experiments, and so may provide a more realistic model of human butchery patterns. Taken together, evidence of cut and percussion mark damage provided by the GIS image analysis is certainly suggestive of early access by hominins at FLK Zinj. This evidence is also consistent with Domínguez-Rodrigo et al.'s (2007) finding that cut marks occur in hot zones on upper and intermediate limb elements, indicating butchery of fully fleshed carcasses.

The GIS analysis of hominin-induced modifications on large bovid limb bones does not match available experimental models, though the analyses for most elements are not robust enough to infer order of access by hominins due to a small sample size of hominin-modified bones. One exception is the radio-ulnae, which preserve cut marks in hot zones, indicating flesh removal by hominins prior to carnivores. The fact that Domínguez-Rodrigo (2007) identified 23% of size 3 and 4 large bovid limbs as bearing cut marks (my own identifications were concordant with his) lends support to an early hominin access scenario for large bovids as well as small bovids.

Extent of Carnivore Involvement at FLK Zinj

Based on the frequency and distribution of carnivore-induced surface damage, the FLK Zinj small- and medium-sized bovids are somewhat more heavily processed by carnivores than those at Kanjera. This is particularly true of the forelimbs. The small/medium hindlimbs are more difficult to compare between sites, as femora from FLK Zinj were not available for GIS analysis. Tibiae are more frequently modified from FLK Zinj with some significant clustering of tooth marks. Metatarsals from FLK Zinj are gnawed on their distal ends rather than on the proximal as they are at Kanjera, but both sites show low frequency, random tooth marking on hindlimbs.

Large bovid femora from FLK Zinj, femora show significant clusters of tooth marks, but their distribution is different from the available experimental models. This is not unexpected given that the experimental models (particularly for dual patterned assemblages: i.e., assemblages modified by multiple actors) are limited, and it is unlikely they have captured the full range of possible tooth marking patterns. There were no large bovid femora available from Kanjera for comparison. The large radio-ulnae from FLK Zinj also show significant tooth mark clustering, but not in a pattern replicated in the carnivore only experimental models (a hammerstone-to-carnivore experimental model is not available). The pattern on the large radio-ulnae is similar to Kanjera but marking is more intensive, and occurs at a higher frequency in the FLK Zinj assemblage. The similarity in tooth mark patterning at FLK Zinj and Kanjera is perhaps suggestive of the involvement of a similar type of carnivore at both sites.

Overall, carnivore tooth marking is more intensive (i.e., bones are more thoroughly processed) at FLK Zinj than is seen at Kanjera. This is demonstrated in the GIS cluster analyses (Fig. 4.5), and is particularly apparent in the forelimbs from FLK Zinj, which show significantly dense clusters of tooth marks. Although tooth mark frequencies are higher at FLK Zinj than at Kanjera, tooth marking to the degree suggested by Blumenschine and colleagues is not supported by this study, nor is the passive scavenging model of carcass access for hominins at FLK Zinj. Tooth mark frequencies reported here still fall within the 95% confidence interval of experimental models (see Blumenschine 1995, Table 3) where carnivore activity followed initial hominin access.

Regarding the question of which carnivore taxa were involved in modifying the FLK Zinj assemblage, the presence of several extinct large felids (*Dinofelis*, *Megantereon*, *Homotherium*) during this time period makes their involvement likely. However, the fact that we do not have extant analogs for these species complicates attempts to reproduce their feeding signatures. In their analysis of multiple Olduvai faunal assemblages, Domínguez-Rodrigo and colleagues (2007) have identified hallmark characteristics of felid involvement in several of the FLK North sites, but not at FLK Zinj. I note that bone preservation patterns observed in the FLK Zinj GIS analyses do not contradict those in my own felid models (Chapter 2), and in fact some isolated tooth marked specimens from FLK Zinj are identical to those produced in my felid feeding experiments (Fig. 4.10). As discussed above, Bunn and Pickering (2010) have argued that the size 3 bovid mortality profile at FLK Zinj does not match that for large felids, and so could not have been formed by hominins scavenging from large felid kills. However, it seems plausible that sabertooth felids adapted to ambush hunting in woodlands would have frequently killed size 3 prime adults as leopards do with smaller prey.

Domínguez-Rodrigo and Barba (2006) have measured tooth pit size in the FLK Zinj assemblage, and have found that tooth pit sizes on cortical bone surfaces fall within the range exhibited by hyenas in experimental assemblages and below the mean for lions. However, in further experiments, Delaney-Rivera et al. (2009) found that tooth pit size on cancellous, epiphyseal bone portions better discriminates between different sized carnivores than pits on cortical bone. In the FLK Zinj assemblage, the range of tooth pit size on cancellous bone overlaps with those reported for hyenas and lions, and the mean is higher than that reported for leopards and cheetahs (Domínguez-Rodrigo and Barba 2006). In a study by Selvaggio and Wilder (2001), which used a different comparative experimental sample, tooth pit size at FLK

Figure 4.10. Carnivore tooth marks at FLK Zinj and in Carolina Tiger Rescue (CTR) experiments. a. distal femur (Cat.# F220) from FLK Zinj, b. distal femur from CTR (Cat.# 221), c. scapula from FLK Zinj, dorsal view (Cat.# C1153), d. scapula from CTR, dorsal view (Cat.# 614).

Zinj on cancellous bone was reported to fall within the range of cheetahs, leopards, and spotted hyenas. It should also be noted that tooth pit sizes on epiphyses at FLK Zinj are within the range of dogs from experiments conducted by Domínguez-Rodrigo and Piqueras (2003). While these studies make identifying specific carnivore taxon difficult due to overlap in the range of pit sizes inflicted by different carnivores, it is clear that the FLK Zinj fauna was modified by a large carnivore.

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

Bone Portion Survivorship and Fragmentation

Interestingly, the more intensive processing of carcasses at FLK Zinj reflected in bone surface modifications is not also reflected in bone preservation and fragmentation patterns. The FLK Zinj fossils show an overall fragmentation pattern similar to that at Kanjera. Bones from both sites are highly fragmented, however, bones from FLK Zinj show an overall better representation of fragments across element portions (including epiphyses), while elements from Kanjera preserve epiphyseal portions less often. One potential explanation for the lower epiphyseal preservation at Kanjera (discussed further in Chapter 3) is the fact that many of the small bovids at Kanjera are juveniles with unfused epiphyses, which are more likely to become removed and destroyed than fused epiphyses.

The fact that fragmentation appears similar at both sites, but percussion marking frequencies are lower at Kanjera, could be explained in several ways. The similarity in fragmentation could be artificial and simply represent a reflection of the degree of completeness needed to enter fragments into GIS (i.e., fragments must be complete enough to allow identification to skeletal element and side; this means small, unidentifiable shaft fragments are not amenable to GIS analysis). This explanation seems unlikely given the available data on bone fragmentation in assemblages from both sites. The epiphysis to shaft ratio in an assemblage can be viewed as an indicator of bone fragmentation due to percussion damage because long bone shafts will be shattered during percussion, while epiphyses will remain intact (Lyman 1994). Ferraro (2007) reports the epiphysis to shaft ratio from Kanjera to be relatively high (0.35, 0.2, and 0.19 for beds KS 1-3 respectively) and broadly consistent with values from experimental hominin only assemblages. Comparable data from FLK Zinj are not available, but Capaldo (1997) reported that two thirds of the long bone portions from FLK Zinj are midshafts, while epiphyses are generally less numerous.

CONCLUSIONS

The evidence presented above clearly indicates early access to fleshed carcasses of small- and medium-sized bovids at FLK Zinj. The larger bovids are more difficult to interpret due to smaller sample size, but they are also suggestive of early access. This interpretation is consistent with bone surface modification patterns and frequencies described here, as well as with evidence of bone surface modifications provided by Domínguez-Rodrigo (2007), skeletal part profile analysis by Faith et al. (2009), and bovid mortality data (Bunn & Pickering, 2010), all indicating early access to carcasses by hominins. The small and medium carcasses may have been acquired through hunting. Carnivores tend to destroy smaller carcasses, so active scavenging is not likely to explain hominin acquisition of relatively complete small bovids.

A potential early access signal is also indicated for the larger bovids at FLK Zinj, although the smaller sample size makes this difficult to interpret as confidently. Evidence for hominin-induced damage on larger bovids is consistent with early access. The lower bone portion survivorship seen in the large bovid limbs may be accounted for simply because there are more nutrients in large bones, so these may have been more thoroughly fragmented by hominins. Hunting cannot be ruled out, but aggressive scavenging of large bovids from felids seems to equally or more plausibly explain early hominin access to large bovids at FLK Zinj.

In comparison with Kanjera, which also shows early hominin access, the FLK Zinj fauna were more intensively processed by both hominins and carnivores. The signature indicating order of access, however, is similar across both sites: hominins had early access to choice carcass portions including meat and marrow. Fragmentation patterns are also similar across both sites. A possible explanation for this discrepancy between level of fragmentation and intensity of bone surface damage at FLK Zinj and Kanjera could be behavioral differences between hominins at the two sites. Perhaps hominins were using a different technique to break open bones at each site. Variation in bone breakage techniques is something that has been observed in ethnoarchaeological contexts (Oliver 1992).

This discussion has only addressed two sites, but it reveals that hominins were adapted to a strategy of hunting smaller animals and perhaps aggressively scavenging larger prey in two different environmental contexts around 2 million years ago. This suggests that Oldowan hominin carcass resource acquisition strategies may be a result of selective pressure for adaptability in coping with environmental variability in the Early Pleistocene rather than directional selection for coping with a specific environment (after Potts 1998, 2012, 2013): such an adaptation perhaps contributed to genus *Homo* successfully occupying and thriving in a range of environments during the later Pleistocene.

CHAPTER 5. Summary and Conclusions

The work presented in this dissertation reports on new experimental research on bone modification patterns and tooth mark frequencies produced by large felids (lions and tigers) and large canids (wolves). This work adds to the growing body of neotaphonomic literature on carnivore bone modification by providing the largest experimental assemblage of bones modified by all of these taxa to date. This experimental work also adds a new dimension to neotaphonomic studies by applying for the first time a GIS image analysis approach (Marean et al. 2001) to characterize bone damage patterns produced by different large carnivores. Further, GIS image analysis is also applied here to model hominin and carnivore produced damage patterns in Blumenschine's (1995) previously studied experimental bone assemblages which represent differing scenarios of carnivore-only, hominin-only and hominin-first access to carcasses.

In the second part of this dissertation, I have used the framework of GIS experimental models to interpret bone modification patterning in the Kanjera South and FLK Zinj archaeofaunal assemblages. The aim of this aspect of my research is to address questions about the order of access by hominins and carnivores to carcass resources at these sites in order to evaluate Oldowan hominin foraging ecology and competitive interactions with carnivores. My results indicate that at Kanjera South, the pattern of bone preservation in small and medium bovids (Bunn's size 1-3a) is similar to GIS-generated models based on experimental bone assemblages that were first butchered and hammerstone fractured by humans and subsequently scavenged by carnivores. The distribution of bone modifications on the Kanjera fauna revealed in the GIS analysis also suggests hominins had early access to small and medium bovids. Large bovids are not as well represented at Kanjera, and so bone damage patterns are difficult to characterize, but evidence presented here suggests hominins may have been scavenging at least some of larger bovids. These results lend further support to the interpretation of hominin early access to prey carcasses that has been made for this site by Ferraro et al. (2013).

The interpretation of the nature of hominin involvement in the well-studied archaeofaunal assemblage from FLK Zinj has been a subject of some disagreement in the literature (Bunn 1986; Oliver 1994; Selvaggio 1994b, 1998; Blumenschine 1995; Capaldo 1997; Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo et al. 2007a; Blumenschine et al. 2007; Pante et al. 2013). The new GIS image analysis data I present here for the FLK Zinj assemblage suggests early access by hominins to fleshed carcasses at FLK Zinj, particularly of smaller prey, which may have been acquired through hunting. Damage patterns on larger carcasses are more difficult to interpret, but are not inconsistent with early access (hunting or aggressive scavenging). Further, a reanalysis of carnivore tooth mark frequencies in the FLK Zinj assemblage corroborates those cited by Domínguez-Rodrigo and colleagues (2007a), lending additional support to an early access scenario for hominins.

This chapter summarizes the main conclusions and provides further discussion of this research presented in the preceding chapters.

CHARACTERIZING PATTERNS OF BONE DAMAGE PRODUCED BY LARGE CARNIVORES

The ability to distinguish between the taphonomic signatures of different large carnivores has wide ranging implications for the way in which Plio-Pleistocene zooarchaeological assemblages are interpreted. These implications include the accuracy with which we can interpret the timing of hominin access to carcasses relative to carnivores as well as the extent of carnivore competition in paleoecosystems. However, our ability to characterize patterns of bone damage produced by various large carnivores has been limited by a lack of consistent methodology applied to study bone damage produced by different taxa. There has also been a limited availability of modern, experimentally-derived samples to characterize such patterns. Recent experimental work by Pobiner (2007) turned our attention to this issue by presenting a system for coding gross bone damage which she used to characterize patterns in a number of carnivore taxa. The work presented in this dissertation builds on the groundwork laid by Pobiner and identifies patterns of bone damage characteristic of large felids and large canids. The work presented here includes the largest experimentally-derived carnivore gnawed assemblages for both large felids and canids, containing a combined sample of over 1,600 specimens representing approximately 97 complete deer (*Odocoileus virginianus*) carcasses fed to wolves and 46 whole or partial deer carcasses fed to large felids. I have used GIS image analysis to characterize patterns of bone surface damage and bone preservation in addition to reporting standard tooth mark frequency data. For the felid assemblage, I also collected data on gross bone damage following Pobiner's (2007) system as well as on flesh availability following felid consumption.

Overall damage patterns identified for the carnivore taxa in this study are presented in Table 5.1. Bone damage patterns based on small carcasses from Blumenschine's spotted hyena assemblage are included in this comparison as well. This table presents a summary of bone damage patterns derived from GIS image analyses as well as direct observation of gross bone damage. I focus here on damage to small carcasses, as the majority of my experimental assemblages consist of size 2 deer carcasses.

When comparing the extent of bone damage among the carnivore taxa in my study, the degree of bone damage falls along a continuum, ranging from large felids (least bone damage) to large canids (more intense damage than felids, but less than spotted hyenas), to spotted hyenas (nearly complete bone fragmentation/destruction of smaller carcasses). Tooth mark frequencies on size 1-2 carcasses fall along this same continuum of large felid (lowest) to spotted hyena (highest) (Table 5.1). Pobiner and Blumenschine (2003, Fig. 2) have hypothesized these same damage capabilities for fossil relatives of these taxa. Red wolves from my study are an exception to the large canid pattern and produce lower tooth mark frequencies than large felids. I summarize differing bone damage patterns created by large felids, wolves, and spotted hyenas in the sections below. I focus on damage to small carcasses, as these make up the bulk of my experimental sample. I discuss damage to both small and large carcasses produced by hyenas. Detailed analyses for wolf and large felid bone modification patterns are fully presented in Chapters 1 and 2. My GIS image analysis for spotted hyena modified bones has a smaller sample size consisting of 8 carcass experiments conducted by Blumenschine, mostly comprised of size 3 carcasses. I more fully describe spotted hyena bone modification patterns here based on my analysis of Blumenschine's assemblage, and I compare these with patterns of damage that have been reported by others for hyenas.

Characteristic Patterns of Large Felid Damage to Size 1-2 Prey

Some characteristic patterns on specific elements that appear to be felid-specific include intensive furrowing on the proximal humerus as well as gnawing on the distal epicondyles which may include furrowing or partial destruction of the epicondyles. The medial epicondyle is sometimes more heavily damaged than the lateral. This pattern is consistent with observations that have been made by Domínguez-Rodrigo et al. (2007a) and Domínguez-Rodrigo (2009), who

Table 5.1. Typical gross bone damage to limbs of size 1-2 carcasses characteristic of different carnivore taxa. Large felid pattern based on the Carolina Tiger Rescue experimental assemblage. Large canid pattern based on experimental assemblage from the Wolf Conservation Society. Hyaenid pattern based on observations of bone damage produced by spotted hyenas in Blumenschine's experimental assemblage (described in Chapter 3). Note that the sample size in Blumenschine's assemblage for small carcasses only consists of 2 experiments. These data represent a summary of patterns identified in the GIS image analyses presented in this dissertation as well as direct observations of gross bone damage. N.d. = no data.

	Large Felid	**Large Canid**	**Hyaenid**
Humerus	- Proximal epiphysis typically shows furrowing and partial or total removal. - Tooth marks may be clustered on the medial epicondyle, which may be partially gnawed away prior to the lateral condyle.	- Proximal epiphysis normally completely removed. - Medial and lateral distal condyles may be furrowed.	n.d.
Radius	- Complete bone normally intact, including distal end which may be tooth marked.	- Distal end normally removed. Gnawed edge may be rounded. More intensive damage may show sections of midshaft levered off from distal end.	n.d.
Ulna	- Olecranon typically gnawed and partially to fully removed.	- Olecranon typically gnawed and partially to fully removed	n.d.
Metacarpal	- Bone is typically fully intact, but tooth marking common on the proximal end. - Proximal end may be destroyed, but distal end remains intact.	- Most of the bone is normally intact, but with distal epiphysis gnawed off.	n.d.
Femur	- Proximal end normally destroyed. Distal end is normally present, but intensively furrowed and may be punctured. Tooth marks cluster at proximal and distal ends.	- Greater trochanter gnawed off and furrowing undercuts femoral head. - Distal end normally completely gnawed off.	- Proximal and distal epiphyses and near epiphyses destroyed. Only shaft fragments remain.
Tibia	- Proximal end may be severely damaged (destroyed or intensively furrowed). - Shaft and distal end typically intact and not tooth marked.	- Proximal end, including up to half of the proximal shaft is normally destroyed. Flakes are levered off the shaft from the proximal end. Distal end intact, but may show tooth pitting.	- Proximal and distal epiphyses destroyed. Only shaft fragments remain.
Metatarsal	- Normally intact. Distal end may be tooth marked.	- Most of the bone is normally intact, but with distal epiphysis gnawed off.	- Distal half destroyed.

argued that gnawing on the medial epicondyle is a felid-specific pattern, differing from hyenas which instead initiate gnawing on the lateral epicondyle. Although I have confirmed this pattern in my felid experimental assemblage, my canid assemblage displays the same pattern of gnawing on the medial epicondyle, so although characteristic of felids, it cannot be considered a felid-specific marker.

Another example of damage that characterizes felids based on my experiments is the degree to which the tibia is damaged. Felids typically furrow and can destroy the proximal epiphysis of the tibia, but leave the shaft and distal end relatively untouched. In contrast, wolves in my experiments routinely completely destroyed the proximal epiphysis and the proximal half of the tibial shaft. Wolves also almost always tooth marked the distal end and sometimes destroyed the distal epiphysis.

On the femur, felids typically furrow and intensively tooth mark the distal epiphysis, but canids in most cases completely destroy the distal end. However, Pobiner's (2007) experiments with wild lions showed a greater degree of damage to the distal femur on small carcasses than mine.

Finally, large felids in my experiments typically left the metapodials complete. They were often not tooth marked and still encased in flesh at the end of feeding. When bone damage did occur, the metacarpals displayed damage at the proximal ends, while damage to the metatarsals occurred on the distal ends. This contrasts with the pattern seen in canids, which begin gnawing from the distal ends of both metacarpals and metatarsals.

In general, my large felid experiments follow Pobiner's in overall damage pattern, but differ in damage degree. Pobiner's sample for small carcasses fed on by wild lions differs in that it is more intensively damaged (for gross bone damage ranking as well as tooth mark frequency).

This may be due to a larger number of individual lions feeding on carcasses in her study compared to the 1 to 3 individuals that fed on carcasses in my study. This shows there is a range of variation large felids are capable of inflicting on bone that may be greater in situations of higher intra-specific competition.

The most diagnostic indicator of felid damage is that overall, bones are complete and not fractured. This pattern is clearly illustrated in Chapter 2 in the GIS image analyses of bone portion survivorship. Felids do not fragment long bone shafts and leave relatively complete bones after feeding. Limb bones show a majority of tooth marking at the ends, while limb shafts are relatively free of marking. Large felids can and sometimes do gnaw on limb bone ends destroying the epiphyses to some degree in size 2 carcasses, but limb bones are rarely fragmented to the degree that hyaenids or even canids are capable of.

Characteristic Patterns of Large Canid Damage to Size 1-2 Prey

Apart from the characteristic differences from felid modification identified above, the general pattern identified in my GIS image analyses of experimental wolf modified assemblages is that long bones are often preserved as cylinders, with destruction and consumption of one or both epiphyses being common. The proximal humerus, greater trochanter of the femur, entire distal epiphysis of the femur, and proximal tibia are almost always destroyed. Distal ends of metapodials are also often destroyed, but not proximal ends. GIS analyses of bone portion survivorship and cluster analyses of tooth marks show that the degree of bone destruction and tooth marking are more intensive in the wolf feeding experiments compared to large felid feeding experiments.

Characteristic Patterns of Spotted Hyena Damage

Observations of patterns of bone damage produced by both captive and wild hyenas have played a prominent role in the neotaphonomic literature. The goal of these studies has been to establish a baseline for the bone processing abilities of hyenas in order to develop criteria for distinguishing accumulations produced by hyenas and hominins (e.g., Binford 1981; Brain 1981; Bunn 1983; Hill 1984, 1989; Klein and Cruz-Uribe 1984; Blumenschine 1988, 1995; Cruz-Uribe 1991; Marean and Spencer 1991; Marean et al. 1992; Blumenschine and Marean 1993; Capaldo and Blumenschine1994; Lupo 1995; Blumenschine et al. 1996; Capaldo 1997, 1998a; Selvaggio and Wilder 2001; Pickering 2002; Pickering et al. 2004). Many of these studies have focused on tooth mark frequency or tooth mark size (e.g., Blumenschine 1995; Selvaggio and Wilder 2001; Faith et al. 2007) or skeletal part frequencies in den assemblages and bone transport behavior of hyenas (Bunn 1983; Lam 1982; Skinner et al. 1986; Kuhn et al. 2009, 2010; Pokines and Kerbis Peterhans 2007; Lansing et al. 2009).

Less research has focused on gross bone damage patterns and hyena-specific damage signatures, but research that has been done, particularly on spotted hyena den assemblages by Sutcliffe (1970) and Hill (1989), shows a consistent pattern for spotted hyena damage that includes:

- Splintering / spiral fracturing of long bones
- Scooping out of cancellous bone
- Presence of tooth punctures
- Gnawed edges on broken limb bones
- Gastric corrosion on small element or element fragments

Pobiner (2007) has most systematically documented gross bone damage produced by spotted hyenas in the wild. Her study was not on a den site, but was in a landscape context, and so damage patterns that she reports might be more characteristic of the expected taphonomic signature hyenas would leave in archaeofaunal assemblages where they scavenged carcass remains processed by hominins. I compare my own observations of Blumenschine's hyena-modified assemblage (also created in the wild in a landscape context) to the gross bone damage patterns documented by Pobiner (2007). The GIS image analyses of bone portion survivorship for Blumenschine's assemblage are illustrated in Appendix A.

Spotted Hyena Bone Damage to Size 1-2 Carcasses

Damage patterns that I observed in the experimental sample of size 1-2 carcasses in Blumenschine's spotted hyena assemblage show a very different pattern from that of felids. The sample amenable to GIS analysis was extremely small (sometimes consisting of a single fragment), in part because hyenas completely consumed or destroyed elements, reducing them to unrecognizable fragments. Blumenschine's original small carcass sample size for these experiments was 2 (Blumenschine 1995, Table 1). My overall observations are concordant with observations of bone damage Pobiner made in her experiments where she noted: "There was virtually nothing left" of the size 1 and 2 carcass parts eaten by spotted hyenas (2007: 131). In Blumenschine's assemblage, only the hind limbs and no forelimbs were preserved. The femur and tibia both preserved only incomplete midshaft cylinders, with epiphyses completely removed (Appendix Figs. A2, A4). The metatarsal preserved only a fragmented proximal end (Appendix Fig. A6).

Spotted Hyena Bone Damage to Size 3-4 Carcasses

For larger, size 3-4 carcasses in Blumenschine's experiments, the sample size included 7 experiments, but I excluded one of them (SER 35) because Blumenschine had documented lion involvement. Spotted hyenas in Blumenschine's experiments normally fragmented the midshafts of large bovid femora (Appendix Fig. A.15) (the midshaft is preserved as a cylinder in one case). The femoral head is preserved in one case, but the greater trochanter was always removed. The distal epiphysis was always completely or partially removed. Pobiner (2007) also found that the femoral head was more likely to survive spotted hyena feeding relative to the greater trochanter. In the large tibiae from Blumenschine's experiments (Appendix Fig. A.16), the epiphyses are always removed, and shafts are preserved as complete or partial cylinders. Pobiner (2007) found the distal part of the tibia preserved in her experiment (but her sample size for that element is 1). The single large bovid metatarsal in Blumenschine's collection is missing the proximal epiphysis and metaphysis, but is otherwise preserved (Appendix Fig. A.16). Hyena-modified large bovid humeri in Blumenschine's experiments (Appendix Fig. A.18) never preserved the proximal epiphysis or metaphysis. The humeral shaft along with distal end was preserved in 1 out of 3 specimens, while the other 2 preserved broken shaft fragments (which refit to form a cylinder). In comparison, Pobiner (2007) found humeri from large ungulates in her experiments ranged from unmodified to destroyed. The ulnae from large bovids in Blumenschine's experiments were completely destroyed. Radial proximal and distal ends were destroyed and only midshaft fragments remained (Appendix Fig. A.19). Pobiner (2007) found the same pattern in her single radio-ulna sample. Finally, the 2 metacarpals in Blumenschine's assemblage are fragmented. The proximal epiphysis is partially removed in one, and all but the distal shaft and metaphysis is destroyed in the other specimen (Appendix Fig. A.20).

Overall, this bone fragmentation pattern shows that spotted hyenas generally inflict significantly more damage on size 3 and 4 carcass parts than large felids do. Long bone midshafts of size 3 carcasses were not fragmented by large felids in my small experimental assemblage, in Pobiner's (2007) experiments, or in Gidna et al.'s (2013) larger study of lion damage to equids. My observations of spotted hyena damage based on Blumenschine's experiments are overall consistent with those made by Pobiner (2007), and display a general pattern in which forelimbs are more thoroughly destroyed than hindlimbs, most epiphyses are destroyed, and bones normally survive as either cylinders or midshaft fragments. Pobiner argued that her results may underestimate the maximum gross bone damage spotted hyenas are capable of inflicting due to artificially low group size in her study. My GIS images may also underestimate bone destruction patterns because unidentifiable shaft fragments cannot be used in GIS analysis because they cannot be placed on the bone template. I should note that many of the individual specimens from Blumenschine's collection were midshaft fragments or splinters of bone that required extensive refitting to determine the complete element before entry into GIS.

In comparison to large felids and large canids, diagnostic patterns of gross bone damage produced by spotted hyenas include their near complete destruction of epiphyses and routine cracking open of bones. Bones from large ungulates typically preserve only midshaft fragments, while those from small carcasses are highly fractured or may even be completely consumed.

Modern hyenas vary in their body size and tooth morphology, and these differences affect the carcass processing abilities of extant species. Spotted hyenas are larger in body size and have more specialized premolars which allow them to more effectively crack open long bones (Werdelin and Solounias 1991). The research devoted to bone damage patterns produced by striped hyenas (*Hyaena hyaena*) and brown hyenas (*Hyaena brunnea*) is comparatively smaller (Richardson 1980; Bartram and Marean 1999; Cruz-Uribe 1991; Kuhn et al. 2009, 2010). Kuhn et al. (2010) has found that compared to spotted hyenas, brown hyenas leave a higher percentage of long bone cylinders (i.e., complete long bone shafts lacking epiphyses). However, this is not a characteristic diagnostic of brown hyenas, as other carnivores (e.g., canids in this study) produce cylinders as well.

INCREASING THE SAMPLE SIZE FOR TOOTH MARK FREQUENCY DATA IN NEOTAPHONOMIC EXPERIMENTS

Large Felid Tooth Mark Frequencies

The experimental work modeling carnivore feeding traces presented in this study significantly increases the size of current neotaphonomic samples available for interpreting carnivore feeding traces in the past. As discussed in Chapter 2, large felid bone modification frequencies have not been modeled as thoroughly as those of hyenas. This study has presented tooth mark frequency data from a sample of over 400 bones derived from size 1 and 2 carcasses fed to lions and tigers, and a smaller sample of 14 bones derived from two large carcasses fed to tigers (see Table 2.3 for sample details). The mean tooth mark frequency produced by large felids on long bone midshafts of size 1 and 2 carcasses in this study was 12.1% (Fig. 5.1, Table 5.2) (mean TM frequency for total NISP = 55.1%). Pobiner (2007) has presented the only other sizeable study measuring wild lion tooth mark frequencies on carcasses of varying size. She reported a midshaft tooth mark frequency for size 1 and 2 carcasses of 58% (see Chapter 2 Table 2.3, Fig. 2.4a), which is considerably higher than my frequency, and outside of the 95% confidence range for my data (see Table 5.2). These differences might be explained due to the potential for a larger number of individuals feeding in Pobiner's experiments in the wild. As my experiments were conducted in a captive setting, the number of carnivores was controlled for and did not exceed 3 individuals.

My experiments modeling large felid damage to size 3 and 4 carcasses only include 2 carcasses, but I present frequency data for comparison (Fig. 5.2, Tables 5.2, 2.3). Midshaft tooth mark frequency in my sample was 58.3% and total NISP tooth mark frequency was 64.3%. Pobiner (2007) reported a midshaft tooth mark frequency of 33% produced by wild lions on large ungulate bones. Gidna et al.'s (2013) study of lion damage to zebra carcasses in the wild reported a total NISP tooth mark frequency similar to mine of 53.6% (they do not report midshaft tooth marking frequency).

Gidna et al. (2013) have criticized the validity of using of captive carnivores to create experimental models, due to the lack of intra-group competition in captive settings, and potential for producing increased bone damage due to boredom chewing. However, my captive tooth mark frequencies on size 1 and 2 carcasses are lower than those produced by wild lions on similar-sized prey in Pobiner's (2007) study. This suggests that captive carnivores can be taken as reliable proxies for wild carnivores in certain settings where controls are introduced to mitigate stereotypical behaviors sometimes observed in captive animals (i.e., controlling for diet, competition, boredom).

Figure 5.1. Percentage of tooth marked long bone midshaft fragments in size 1-2 carcasses from experimental carnivore-modified assemblages.
Large felids are tigers and lions described in Chapter 2. Wolf experiments are described in Chapter 1. Hyena data are from Blumenschine's "carnivore only" spotted hyena assemblage. Frequency for hyenas originally reported in Blumenschine (1995). Error bars represent 95% confidence intervals. Data from Table 5.2.

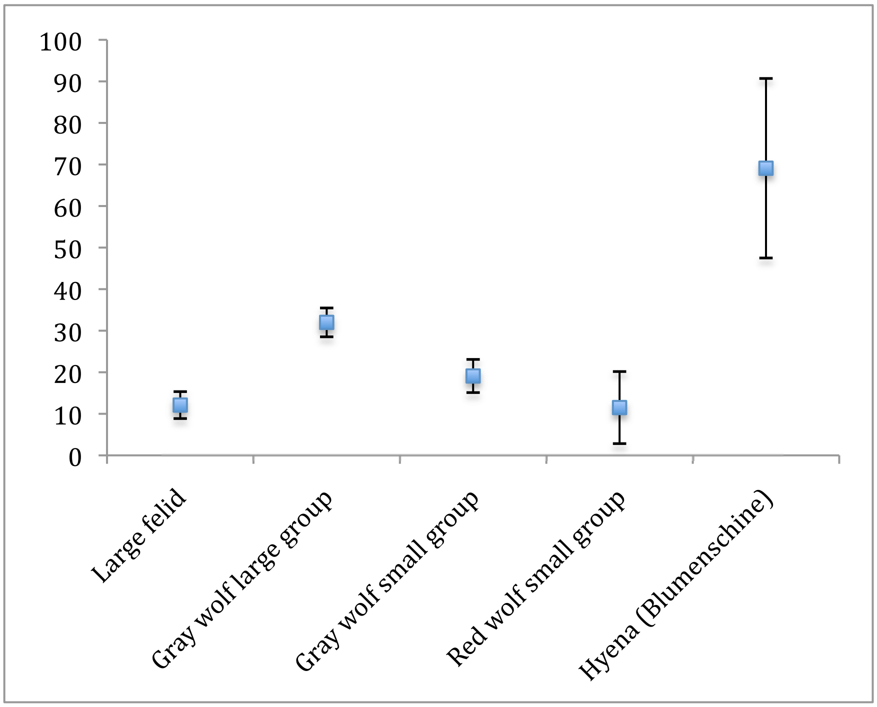


Figure 5.2. Percentage of tooth marked long bone midshaft fragments in size 3-4 carcasses from experimental carnivore-modified assemblages.
Large felids are tigers and lions described in Chapter 2. Wolf experiments are described in Chapter 1. Hyena data are for Blumenschine's "carnivore only" spotted hyena assemblage. Frequency for hyenas originally reported in Blumenschine (1995). Error bars represent 95% confidence intervals. Data from Table 5.2.

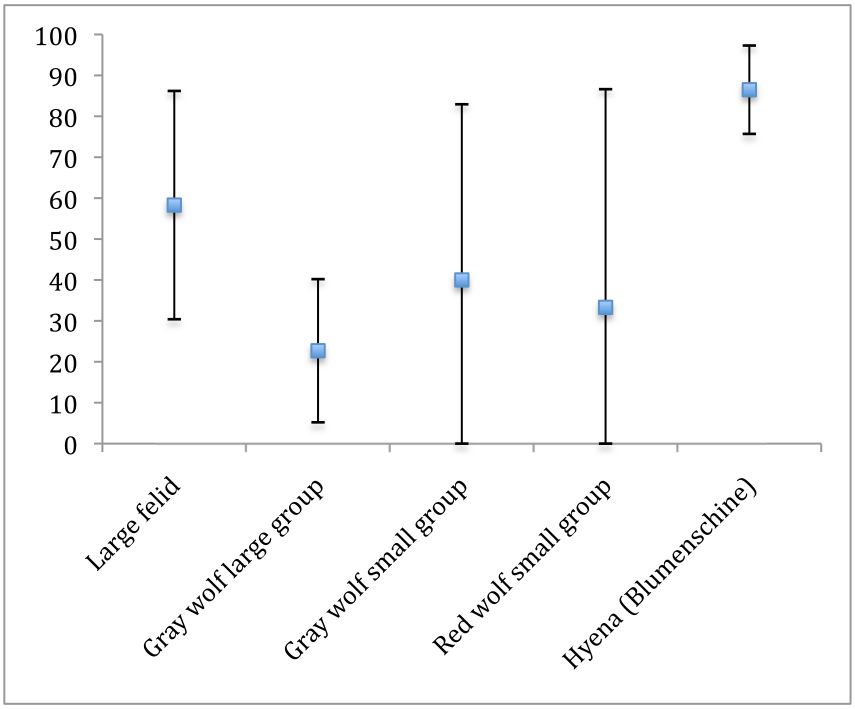


Table 5.2. Percentage of tooth marked long bone midshaft fragments in experimental carnivore-modified assemblages. Number in parentheses represents 95% confidence interval.

	Size 1-2 Midshaft TM %	Size 3-4 Midshaft TM %
Large felid	12.1 (±3.24)	58.3 (±27.9)
Gray wolf large group	32 (±3.47)	22.7 (±17.5)
Gray wolf small group	19.1 (±3.99)	40 (±42.94)
Red wolf small group	11.5 (±8.67)	33.3 (±53.33)
Hyena (Blumenschine)	69.1 (47.5-90.7)*	86.5 (75.7-97.3)*

* Data reported by Blumenschine (1995)

Large Canid Tooth Mark Frequencies

I have presented tooth mark frequencies for large canids made by different groups of study animals separately. These include a large group of gray wolves (15 individuals), small group of gray wolves (2 individuals), and small group of red wolves (2 individuals). As wolves and other large canids are typically pack hunters (Ewer 1974; Creel and Creel 1995), the bone damage frequency produced by the large group in my study is more likely to realistically model the extent of damage these carnivores will produce. Smaller groups model damage produced by these species in contexts of lower competition.

Tooth mark frequencies on midshafts of size 1 and 2 bones occur at a frequency of 32%, which is intermediate between the frequency of tooth marks produced on similarly sized long bone midshafts by large felids (12%) and spotted hyenas (69%) (Fig. 5.1). As expected, midshaft tooth mark frequencies produced by wolf pairs (12-19%) were lower than in the large group (32%).

On larger-sized carcasses fed on by different wolf groups, a small sample size (combined NISP of 30; see Chapter 1 Table 1.3 for details) makes tooth mark frequencies difficult to interpret with confidence. However, tooth marked midshafts in all three wolf groups occur at frequencies below those in my large felid study. Total tooth marked NISP for all wolf groups, however, was always above 75% (Table 1.3).

Summary of Differences in Damage to Bones Produced by Large Felids, Wolves, and Spotted Hyenas

Bone portion survivorship and tooth mark clustering patterns are best viewed as a continuum in which large felids process bone less thoroughly than hyaenids, and large canids are intermediate in their processing abilities. When consuming small to medium sized carcasses, large felids do not generally fragment long bone shafts, but instead gnaw on and sometimes destroy low density epiphyseal portions, leaving complete bone cylinders with one or both ends missing. Felids may tooth mark long bone shafts, but not nearly as intensively as spotted hyenas do. The frequency of tooth marking imparted by large felids on small carcasses is lower than that produced by hyaenids, while wolf tooth mark frequencies fall between the two (Fig. 5.1).

Diagnostic damage produced by spotted hyenas includes destruction of epiphyses, and routine breaking open of bones.

USING NEOTAPHONOMIC MODELS TO INTERPRET FEEDING SIGNATURES OF EXTINCT FELIDS IN ARCHAEOFAUNAL ASSEMBLAGES

Adaptive Patterns in Sabertooth Felids

One problem with attempts to interpret behaviors of extinct carnivores using experimental models based on modern taxa is that modern carnivores may not provide direct behavioral analogs. This is an issue that has been identified by Domínguez-Rodrigo (2012), although it is not always applied in experimental studies. In addition to modern lions, the large carnivore guild in the Early Pleistocene of East Africa included three now extinct machairodont (sabertooth) felids (*Dinofelis*, *Megantereon*, *Homotherium*). Fossil remains of modern lions as well as *Dinofelis* and *Megantereon* are found in Olduvai Bed I (Lewis 1997), and their involvement in modifying the ungulate fauna there is likely. *Homotherium* is known from the same time period, but remains of this genus have not been found at Olduvai (Werdelin and Sanders 2010).

Studies of sabertooth felid postcranial (Lewis 1997; Werdelin and Lewis 2001) and dental morphology (Emerson and Radinsky 1980; Marean 1989, Van Valkenburgh et al. 1990; Biknevicius et al. 1996; Biknevicius and Van Valkenburgh 1996; Hartstone-Rose and Wahl 2008; Hartstone-Rose 2011) have attempted to reconstruct the adaptive patterns of these extinct felids in some detail. Overall, characteristics of the machairodont felids suggest they specialized on large prey, perhaps larger than modern large felids (Emerson and Radinsky 1980; Marean and Ehrhardt 1995). Ecomorpholocal studies of the postcrania of *Dinofelis* and *Megantereon* suggests these taxa were probably ambush predators that inhabited relatively closed environments (Werdelin and Lewis 2001). *Homotherium*, in contrast, may have been a pack hunter (Lewis 1997).

Characteristics of sabertooth dentition suggest that like extant large felids, sabertooths were likely flesh-specialists and appear to have lacked adaptations for bone crunching in their postcanine dentition (Hartstone-Rose and Wahl 2008; Hartstone-Rose 2011). Apart from the enlarged canine, sabertooth felid anterior dentition differs from that of modern large felids in having procumbent incisors, which is a feature more similar to modern canids than modern felids. This indicates the sabertooth mode of defleshing carcasses may also have been more similar to that of canids (Biknevicius et al. 1996; Hartsone-Rose 2008). A differing mode of carcass defleshing may have had an effect on the frequency with which sabertooth felids produced tooth marks on bone. My experimental research has shown that large canids impart higher frequencies of tooth marks than large felids at least on small carcasses. The small sample size in my assemblage of large carcasses prevents a determination of whether this is the case for large carcasses as well. Marean and Ehrhardt (1995) have provided direct evidence for the carcass processing abilities of sabertooth felids in their analysis of the fauna from Friesenhan Cave, a sabertooth den site in North America attributed to *Homotherium*. Their analysis demonstrated that at least *Homotherium* was capable inflicting tooth marks on bones of large mammals at frequencies of up to 54% (total NISP tooth marked was 21%).

Implications for Potential Early Hominin Scavenging Opportunities from Felids

Adaptations in the extinct felids summarized above (and described in detail in Chapter 2) have implications for the type of competitive interactions early hominins may have engaged in with these felids during the Plio-Pleistocene. It has been suggested that as hominins began to incorporate meat into their diets at approximately 2.6 Ma (Semaw et al. 2003) there was a transition through a scavenging phase prior to the advent of hunting (see further discussion in Chapter 4). One hypothesis is that a scavenging niche for early hominins focused on within-bone tissues could have been made possible by the greater diversity of flesh-specialist felids in closed habitat environments (Blumenschine 1987; Marean 1989). If sabertooth felids were more hypercarnivorous than modern felids and lacked the adaptations necessary to fully utilize all carcass portions, this could have provided a scavenging niche for hominins focused on extracting marrow. However, recent work by Hartstone-Rose (2008, 2011; Hartstone Rose and Wahl 2008) has provided evidence that sabertooths were not more hypercarnivorous than modern felids and thus would probably not have provided higher quality scavengable carcasses than extant felids do.

Domínguez-Rodrigo (1999, Domínguez-Rodrigo et al. 2007a) has also argued based on availability of flesh on carcasses abandoned by lions in modern habitats, that scavenging flesh from felid kills would not be a reliable strategy, as only marrow resources remain. My study of flesh availability in the Carolina Tiger Rescue experiments (presented in Chapter 2) demonstrated a similar pattern of nearly complete defleshing of all upper limb bones (but see Pobiner 2007). Blumenschine (1987) found that the degree to which carcasses are consumed in the wild is dependant on ecological setting. In his studies, Blumenschine found that lion kills in open grasslands were more thoroughly destroyed because other carnivores were also present at the site (e.g., hyenas, jackals). In woodlands, it takes longer for other competitor species to discover carcasses, and so carcasses may persist for longer periods untouched. Current evidence seems to suggest that scavenging opportunities for large ungulate carcasses in woodlands may have been available to Plio-Pleistocene hominins, but these opportunities were likely restricted to marrow and not likely to involve access to flesh. These are opportunities that would have been available to hominins passively scavenging after lions had abandoned their kills. On the other hand, aggressive scavenging, where hominins drove solitary large felids away from carcasses could potentially have yielded significantly greater quantities of flesh.

Some Thoughts on Interpreting Past Felid Taphonomic Signatures

An examination of the paleoecology and morphological feeding adaptations reconstructed for extinct felids compared with modern felids brings up two important considerations for interpreting past felid taphonomic signatures.

1. Hunting behaviors of extinct, sabertooth felids may have been somewhat different than in extant felids. Prey was probably grasped with their procumbent anterior teeth, and some flesh was likely removed with the incisors in a way similar to modern canids. Elongated canines were probably used to make long slashes during prey killing, potentially allowing extinct felids to have taken larger prey than modern felids. It follows from this that the higher taxonomic diversity in Plio-Pleistocene large felids which specialized on taking medium to large ungulate prey could have provided a scavenging niche for hominins focused on marrow extraction, but not flesh. This niche is more likely to have been available in closed, wooded environments, as carcass persistence would be longer. Aggressive scavenging by hominins from solitary sabertooth individuals would have provided greater amounts of flesh.
2. Although hunting behaviors and prey selection may have differed in extinct felids, thus affecting scavengable carcass yield for hominins, tooth mark patterns and frequencies on bone consumed by extinct felids are likely to have been similar to the damage modern felids impart. This is because the bulk of defleshing is done with the postcanine teeth in modern felids, and the function of the postcanine teeth in extinct felids has been

reconstructed in a similar way. One difference is that some defleshing in extinct felids may have also been done with the incisors in a similar fashion to large canids. Given this, when attempting to recognize signatures of extinct felid bone damage in archaeofaunal assemblages, the model presented here based on modern large felids should provide a realistic analog, but extinct felids may have been capable of creating a slightly greater degree of damage, perhaps approaching the extent of damage produced by large canids (see Chapter 1). Damage patterns produced by large felids and canids are similar in overall pattern, but differ in degree. Marean and Ehrhardt (1995) found 21% of the NISP tooth marked in the Friesenhahn *Homotherium* den assemblage, which is less than that documented in my canid experiments. Bones of larger animals at Friesenhan, however, were tooth marked at higher frequencies (up to 54%), suggesting that sabertooths were capable of producing high tooth mark frequencies within the range of canids and hyaenids. Therefore, feeding traces based on modern large felids should be interpreted as representing the low end of the spectrum of bone damage that could have been inflicted by large felids in the past.

HOMININ CARCASS ACCESS AT KANJERA SOUTH AND FLK ZINJ

In the second part of this dissertation, I used GIS image analysis to characterize bone portion survivorship and bone surface damage patterns in the Kanjera South, Kenya (ca. 2 Ma) and FLK Zinj, Tanzania (ca. 1.8 Ma) faunal assemblages. I analyze these within the framework of the neotaphonomic work I have presented. The aim of this research has been to address questions about the order of access by hominins and carnivores to carcass resources at these sites, as well as to determine if there are any subtle differences in patterning that may indicate different behavioral strategies practiced by hominins in the different environmental contexts at these two sites.

Frequency of Bone Surface Modifications at Kanjera and FLK Zinj

Carnivore Tooth Mark Frequencies

The frequency and location of carnivore tooth marks on skeletal remains can provide important information regarding the timing of access to carcasses by carnivores. Ferraro et al. (2013) have reported tooth mark frequencies on midshaft specimens in the total Kanjera assemblage (summed beds KS-1- KS-3, all size classes) to be between 8 and 14%. My own independently calculated tooth mark frequency for the Kanjera South assemblage (14%) (Fig. 5.3) is within the range reported by Ferraro et al. (2013). These frequencies all fall within or slightly below the range of experimental “hominin-first” models where carnivores had secondary access to carcass remains defleshed and demarrowed by humans (5-15% of NISP tooth marked) (Blumenschine 1995; Capaldo 1998b; Marean et al. 2000). Tooth mark frequencies on midshafts from Kanjera are well below the range in experimental “carnivore-only” models, in which carnivores including spotted hyenas had sole access (>75% of NISP tooth marked) (Blumenschine 1995), although they are within the range produced by large felids in my experimental work (11-58%).

There has been considerable disagreement in the literature over tooth marking frequencies in the FLK Zinj assemblage (Domínguez-Rodrigo and Barba 2006; Blumenschine et al. 2007; see also Oliver 1994). Blumenschine (1995) reported an assemblage-wide tooth mark frequency of 61% of the NISP. Domínguez-Rodrigo and colleagues have reported comparatively low tooth mark frequencies at FLK Zinj (17% of NISP). Domínguez-Rodrigo and Barba (2006) argued that some bone surface modifications originally identified as tooth marks by Blumenschine were instead marks produced by biochemical processes, and that misidentification of biochemical marks as tooth marks was the cause of the higher tooth mark frequencies in Blumenschine's analysis. I independently calculated tooth mark frequencies in the FLK Zinj assemblage to be 24% of the NISP, much more consistent with the level of carnivore damage that Domínguez-Rodrigo documented. In the shared sample analyzed by both Domínguez-Rodrigo and myself, my identification showed 92.5% concordance with his. This suggests that biochemical damage could potentially have been a factor in the higher tooth mark frequencies reported by Blumenschine. Tooth mark frequencies I report here for FLK Zinj fall within the 95% confidence interval of experimental models where carnivore activity followed initial hominin access (see Blumenschine 1995, Table 3).

Frequencies of Hominin Produced Damage

The frequency of percussion marking (6%) and cut marking (4.7%) that I report for assemblage-wide NISP at Kanjera South is within the range reported by Ferraro et al. (2013). For the FLK Zinj assemblage, there is more agreement between observers on the frequency of hominin produced damage (see Chapter 4 Table 4.4), and my frequencies of 15.5% (CM) and 23.1% (PM) are in broad agreement with others.

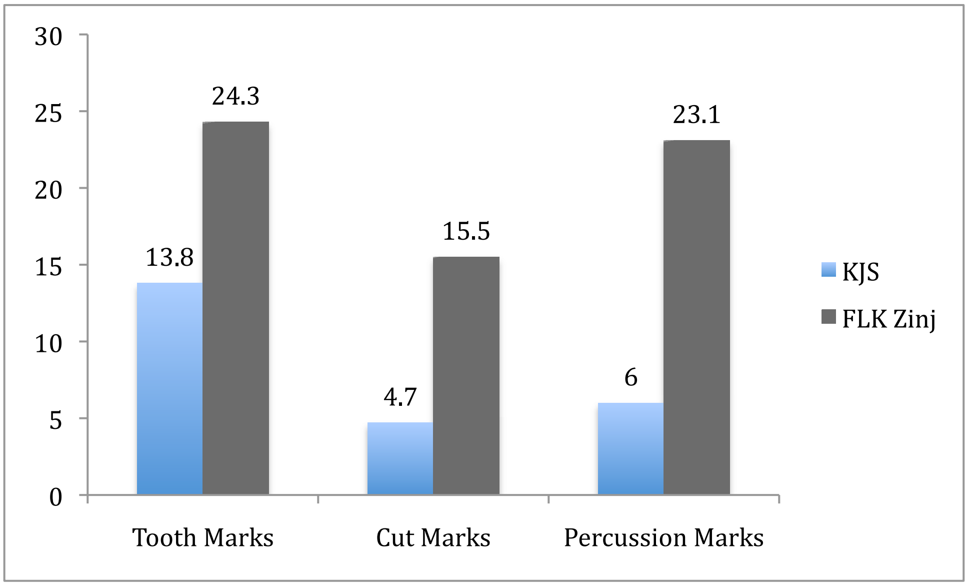
As Figure 5.3 illustrates, the frequency of both hominin- and carnivore-induced damage is higher in the FLK Zinj assemblage than at Kanjera South, indicating more thorough processing of carcasses by both hominins and carnivores at FLK Zinj despite the evidence for early hominin access at both sites.

GIS Image Analysis of Bone Damage Patterns at Kanjera and FLK Zinj

Hot Zones

The GIS mapping of cut mark distribution in the Kanjera assemblage demonstrates that the majority of marks on size 1-3a bovids (9 out of 16 marks: 56%) fall within the "hot zone" areas defined by Domínguez-Rodrigo et al. (2007a) as areas where flesh typically does not survive felid consumption. My own experiment of flesh availability following large felid consumption presented in Chapter 2 confirms the pattern observed by Domínguez-Rodrigo (1999), where upper and intermediate limb elements are typically completely defleshed and flesh scraps remain only at the joints. The presence of cut marks in these hot zones is suggestive of early access by hominins to size 1-3a carcasses at Kanjera. Cut marks do not occur in hot zones on large bovids at Kanjera South, but the sample size of size 3b bovids is small.

Figure 5.3. Summary of bone surface modification frequencies at Kanjera South and FLK Zinj. Frequency data are for assemblage-wide NISP calculated in this study. See Chapters 3 and 4 for detailed breakdown of these frequencies.



In comparison, Domínguez-Rodrigo et al. (2007a) have shown that in the FLK Zinj assemblage cut marks also fall within hot zones. They report 40% of marks on the femora and 20% of marks in the tibiae occur in hot zones, suggesting early access by hominins to fleshed carcasses at this site as well.

GIS Cluster Analyses

The GIS cluster analyses presented for the FLK Zinj assemblage demonstrate that on small and medium bovids, there is a random, unclustered tooth mark distribution on most limb bones. Exceptions are some areas of the humerus, tibia, and metacarpals which do show significantly dense clusters of tooth marks. These clusters are most consistent with those from GIS models of carnivore secondary access and not carnivore only access.

For larger bovids at FLK Zinj, the radius and femur were the only elements amenable to GIS analysis, and both display significantly dense clusters of tooth marks. A significant cluster of tooth marks appears on the proximal radius, but experimental models for large bovid radii are not available for comparison. The distribution of tooth mark clusters on the femur does not coincide with those in experimental models which depict “carnivore only” and “hominin-to-carnivore scenarios”. This is not unexpected given that the experimental models (particularly for dual patterned assemblages modified by multiple actors) are limited, and it is unlikely they have captured the full range of possible tooth marking patterns.

Tooth marking in the Kanjera assemblage does not occur at a high enough frequency to conduct cluster analyses on. However, a comparison of the distribution of cut marks in the Kanjera size 1-3a bovids compared with a GIS cluster analysis of cut marks from models of experimental butchery using stone tools on hind limbs shows that most cut marks fall within the areas of significantly dense cut mark clustering. This further line of evidence suggests hominins were butchering fleshed carcasses of small and medium bovids at Kanjera.

GIS Bone Portion Survivorship

Based on GIS image analyses of bone portion survivorship, bones from both FLK Zinj and Kanjera are highly fragmented. However, bones from FLK Zinj show an overall better representation of fragments across element portions (including epiphyses), while elements from Kanjera preserve epiphyseal portions less often. One potential explanation for the lower epiphyseal preservation at Kanjera (discussed further in Chapter 3) is the fact that a number of the small bovids (24% of size 1 bovids), at Kanjera are juveniles with unfused epiphyses, which are less likely to survive than fused epiphyses.

One possible explanation for the high fragmentation levels at both sites, but lower percussion mark frequencies at Kanjera compared with FLK Zinj, could be that hominins were breaking bones in a different way at Kanjera. For example, because prey carcasses were generally smaller at Kanjera, hominins may have simply struck bones against an anvil to break them open rather than percussing them with a hammerstone on an anvil. This is a behavior that has been documented in the modern Hadza hunter-gatherers of Tanzania (Oliver 1992). Striking bones against an anvil may be less likely to leave the percussion mark damage found on bones broken using a hammerstone. If this were the case, hominins may have been accessing marrow just as frequently at Kanjera, but not leaving the expected taphonomic signature. Oliver (1992) has observed modern Hadza hunter-gatherers in Tanzania using this technique to break open bones in addition to using a hammerstone. Another possibility for the difference in percussion mark frequenies could be use of a different raw material for hammers and anvils at the sites (Pickering and Egeland 2006). Further experimentation would be required to test these ideas.

The GIS bone preservation analyses from both FLK Zinj and Kanjera are on average most consistent with experimental models where hominins fragmented long bone midshafts and carnivores removed or destroyed epiphyses to a varying level (or degree). When compared to experimental models, epiphyseal deletion at FLK Zinj is often lower than in the hammerstone-to-carnivore models, perhaps because Blumenschine's (1995) experiments (which these experimental models are based on) were conducted in the extremely competitive Serengeti ecosystem. The intensity of competition among members of the carnivore guild in the Serengeti may not provide an appropriate analog for competitive dynamics in the paleo-ecosystems at Kanjera South or FLK Zinj (Tappen 1995, 2001). Further, in Blumenschine's experiments, spotted hyenas are the only scavenger species. Secondary involvement by other non-bone crunching large carnivores, such as canids or felids, has not been experimentally modeled.

Competition Levels at FLK Zinj and Kanjera South

The differences seen in taphonomic signatures between the FLK Zinj and Kanjera faunal assemblages are likely due to differing paleoecological variables at these sites including carnivore and herbivore guild structure and biomass, hominin population size, competition level, and availability of amenities to hominins such as stone raw material, water, and shade trees. The competition level in a given environment is largely determined by predator-to-prey ratio and habitat type (Sinclair and Norton-Griffiths 1979; Blumenschine, 1987; Blumenschine et al. 2004). Modern open habitats typically experience higher levels of competition because visibility (and thus, potential for identifying carcasses) is good, whereas carcasses may persist hidden in brush for longer periods in more wooded environments (Blumenschine 1987; Blumenschine et al. 1994; Domínguez-Rodrigo 2001). Because Kanjera was a more open environment, and FLK Zinj a wooded environment, the apparently higher competition at FLK Zinj (indicated by more intensive carcass processing by hominins and carnivores) initially seems difficult to explain. However, the paleoenvironment of lower Bed I has no exact modern correlate, and so models of competition based specifically on modern savanna ecosystems may not be completely appropriate. The greater diversity of bovids (including now-extinct large bovids *Pelorovis* and *Megalotragus*) and large carnivores during the Plio-Pleistocene including extinct sabertooth felids (*Dinofelis*, *Megantereon*, and *Homotherium*) and an extinct hyaenid (*Chasmaporthetes*) suggests predatory opportunities could have been higher than in modern savanna ecosystems (Domínguez-Rodrigo et al. 2007a). More opportunities to hunt and scavenge may have existed due to higher herbivore biomass as well as greater niche partitioning among specialized carnivores (Plummer 2004). Marean (1989) has also that argued scavenging opportunities could have been greater in the past, particularly due to the likelihood of sabertooth felids yielding reliable scavenging opportunities in wooded environments. However, based on their analysis of the Friesenhan *Homotherium* den assemblage, Marean and Erhardt (1995) subsequently argued that the carcass processing and transport abilities of sabertooths may have been greater than previous studies have recognized, meaning they would leave less scavengable carcass remnants. Hartstone-Rose (2008) has also argued based on dental morphology of extinct felids (see Chapter 2), that they were not more flesh-specialized than modern large felids, and so were not capable of producing higher quality scavengable carcasses than modern felids do. Still, similar to modern large felids, sabertooth felids would have produced carcasses with scavengable within-bone nutrients.

Were Hominins Hunting or Scavenging at Kanjera South and FLK Zinj?

Evidence from the GIS image analysis of bone fragmentation patterns and the distribution of bone surface modifications in the archaeofaunal assemblage from Kanjera South presented here suggests that hominins had relatively early access to carcasses at this site. Cut marks occur in hot zones on small bovid limb bones, indicating access to fleshed carcasses by hominins. The low frequency and random distribution of carnivore tooth marking at Kanjera suggests carnivore secondary access. Relative to GIS models of “carnivore only” scenarios, the higher preservation of epiphyses at Kanjera suggests carnivores were not forming or greatly modifying the assemblage. Although carnivores were present (fossils of size 2 and 3 felids, hyenid indet., and *Crocuta* cf. *dietrichi* have been found; see Plummer et al. 2009a), there seems to have been lower on-site competition at Kanjera compared to FLK Zinj.

The evidence presented here from the GIS image analysis of the FLK Zinj fauna, along with my reanalysis of bone surface modification frequencies from this site, is consistent with an interpretation of early access by hominins to fleshed carcasses at FLK Zinj. This evidence is also consistent with studies of bone surface modification by Domínguez-Rodrigo et al. (2007a), skeletal part profile analysis by Faith et al. (2009), and bovid mortality data provided by Bunn and Pickering (2010), which all indicate early access by hominins. The question then remains: how did hominins at FLK Zinj and Kanjera South acquire fleshy carcasses? Hunting and/or aggressive scavenging are two potential methods of acquiring complete carcasses.

Oldowan hominins had a relatively limited tool kit consisting of cores and flakes, and there is no evidence for hunting technology (i.e., bows and arrows, spears) in the archaeological record before about 500,000 years ago (Wilkins et al. 2012). However, Bunn and Pickering (2010) have argued that the absence of hunting technology does not necessarily indicate an absence of hunting capability. Additionally, the absence of hunting technology in the Oldowan could be a taphonomic issue. We don’t have a record of tools made out of perishable materials such as wood (Plummer 2004). Lemorini et al. (in review) have demonstrated that use-wear on stone tools from Kanjera South shows they were used for cutting and scraping wood, among other things. They argue that the purpose of this could have been for fashioning hunting spears.

If Oldowan hominins were hunting, they might have accomplished this through endurance running / persistence hunting (sensu Bramble and Leiberman 2004) or by ambushing prey. Both of these techniques would lead to a pattern of bone surface damage indicating early access, which is exactly what is found in the FLK Zinj assemblage. What might distinguish one from the other is evidence from bovid mortality profiles. As discussed in Chapter 4, bovid mortality profile evidence provided by Bunn and Pickering (2010) does not support an endurance running technique for hunting large bovids at FLK Zinj. FLK Zinj large bovids show a mortality pattern consisting of prime-aged adults. This is a pattern normally seen only in human produced mortality profiles (Steele 2003). The small bovids from FLK Zinj show a different mortality pattern consisting of mainly older individuals, which is the pattern seen for cursorial predators (such as wolves, African wild dogs and spotted hyenas), and the one expected to result from endurance running (Stiner 1990; Steele 2003).

Persistence Hunting

Ethnographic research has documented persistence hunting through endurance running in the modern Kua people in the central Kalahari (Lee 1979; Liebenberg 2006) as well as by some Native American tribes. The Tarahumara of northern Mexico have been documented chasing deer to exhaustion and then killing them by hand (Pennington 1963). The Paiutes and Navajo of the southwestern United States have also been reported to have used this method in some instances to hunt pronghorn antelope (Lowie 1924). Reliable ethnographic data on mortality profiles resulting from persistence hunting are not available, but anecdotal data on the Kua reported by Liebenberg (2006) suggest that small animals are most frequently run down.

Seasonality influences when the Kua will persistence hunt larger animals, choosing to focus on species when they are most nutritionally compromised or when the substrate in their environment makes running must difficult. Kua persistence hunt kudu bulls more frequently because they tire more easily due to their heavy horns, while kudu cows are normally ignored by the Kua unless they are wounded or pregnant.

Bunn and Pickering (2010) have argued that endurance running / persistence hunting is not a good explanation for the early access pattern at FLK Zinj. They cite their own ethnographic observations that modern Kua hunters sometimes walk small bovids to exhaustion in sparsely vegetated environments (Bunn and Pickering 2010), so running is not necessarily required. Bunn and Pickering (2010: 402) have argued that in the more wooded paleoenvironment at Olduvai, persistence hunting through endurance running would require "even greater tracking skills beyond those possessed by modern foragers" to be successful. This might have been true in the case of the wooded environment at FLK Zinj, but an endurance running hunting strategy may have been more feasible in an open environment like Kanjera.

If Oldowan hominins at FLK Zinj were not persistence hunting, perhaps they were ambushing their prey. Bunn and Pickering (2010) have argued that hominins may have waited in trees near game trails and speared prey that came in close proximity to them. There is currently no evidence for lethal weaponry in the archaeological record at this time. However, Bunn and Pickering believe wooden spears are a possibility, given use-wear evidence for wood working on artifacts from Koobi Fora (Keeley and Toth 1981) at ca. 1.5 Ma. Use-wear indicating woodworking is also found on even older artifacts from Kanjera South (Lemorini et al. 2009; Lemorini et al., in review). Phytoliths from the edges of handaxes from Peninj, Tanzania, a site roughly coeval with FLK Zinj also suggest wood working (Domínguez-Rodrigo et al. 2001).

Further, observations have been made in the wild of chimpanzees making and using sharpened sticks to stab bush babies (Pruetz and Bertolani 2007). If chimpanzees recognize that a sharpened stick can be used to stab prey, and modify and utilize such sticks for this purpose, it is not a stretch to imagine hominins using stone tools to shape branches in order to form thrusting spears.

Aggressive Scavenging

Aggressive (power) scavenging from felid kills is an alternative explanation that could account for early hominin access to bovids at FLK Zinj. The idea that hominins were scavenging from large felid kills is something that was originally suggested by Blumenschine and colleagues (Blumenschine 1995; Selvaggio 1998), although Domínguez-Rodrigo and colleagues (Domínguez-Rodrigo and Barba 2006) provide convincing evidence against passive scavenging from large felids at FLK Zinj. It has also been suggested by Cavallo and Blumenschine (1989) that hominins may have passively scavenged smaller carcasses from tree stored leopard kills. Bunn and Pickering (2010) also argue that the prime-dominated bovid mortality profile at FLK Zinj does not match that of modern lions (as reported by Schaller 1972), which are less selective and tend to be biased toward older individuals, and so the FLK Zinj mortality profile cannot represent remains of large felid kills scavenged by hominins. However, it should be noted that in their examination of bovid mortality in the arguably non-anthropogenic "background" scatter on the Olduvai paleolandscape (which is thought to be accumulated to a large extent by extinct felids), Bunn and Pickering found that it overlaps with the mortality pattern at FLK Zinj more so than the pattern for modern felids. This "background" scatter consists of the FLK N 1-2, FLK N 6, and FLK NN 2 sites, which Domínguez-Rodrigo et al. (2007a) have argued were primarily accumulated by extinct felids. Given that a greater diversity of large felids existed in the past, we should not be too quick to assume that modern lions are an identical proxy for extinct felids which likely had different feeding ecologies. *Homotherium*, an extinct sabertooth felid that rivaled modern lions in size, has been reconstructed as a possible pack hunter and so may not have provided safe scavenging opportunities for hominins (Lewis 1997). However, the extinct sabertooth felid *Megantereon* and the “false sabertooth” *Dinofelis* were smaller in size, and probably solitary, ambush predators in mixed or closed habitats (Werdelin and Lewis 2001). It has also been suggested that sabertooths may have taken larger prey sizes (medium to large ungulates) because they could have made a larger killing slash with their canine than modern felids can (Emerson and Radinsky 1980). Given these differences in the large carnivore guild structure, evidence that the FLK Zinj bovid mortality profile closely resembles the apparently felid-accumulated background scatter at Olduvai, evidence for early access to fleshed carcasses presented in this chapter and by others, and evidence for isolated damage patterns that resemble those of modern felids (Chapter 4 Fig. 4.10), it seems conceivable that a power scavenging scenario of hominins stealing large prey from sabertooth felids could also have led to the mortality profile seen in the FLK Zinj assemblage.

Interestingly, although evidence indicates early access for hominins at both FLK Zinj and Kanjera, the bovid mortality pattern at Kanjera is different. A complete analysis of mortality patterns is not yet available for Kanjera, but an overall juvenile-dominated pattern is apparent (Ferraro 2007). Based on dental attrition, 13 out of 26 bovid individuals in Bed KS-1 at Kanjera were juvenile (Plummer pers. comm.). A mortality pattern including very young or old individuals is one that has been associated with persistence hunting by cursorial predators (Bertram 1979). Evidence indicates that hominins at Kanjera were acquiring fleshed carcasses; however, they may have been acquiring these carcasses in a different way than hominins at FLK

Zinj. In a grassland setting like Kanjera, it would probably have been harder to ambush prey than in a wooded environment like FLK Zinj. A mortality profile showing an abundance of young size 1-3a individuals could indicate an endurance running / persistence hunting strategy for small bovids at Kanjera. Alternatively, the juvenile-dominated pattern could represent an effect of seasonality, where an abundance of juveniles was simply available for hunting at certain times of the year. Further research into seasonality, for example, examining bovid dental histology, would be necessary to tease apart these alternatives.

For the larger bovids at Kanjera, an interpretation of early access is not as straightforward as for the smaller bovids. Ferraro et al. (2013) documented differences in skeletal element abundances at Kanjera showing even representations for small bovids (indicating transport of whole carcasses), but an abundance of limb and head elements for medium-sized bovids. This suggests a more mixed history in terms of acquisition of medium sized carcasses, where perhaps there was a mix of active and more passive scavenging at Kanjera.

Conclusions About Carnivore and Hominin Activities at Kanjera and FLK Zinj

The GIS image analysis of the Kanjera South and FLK Zinj bovid fauna presented here suggests that hominins had early access to fleshed carcasses at both sites. The results of new analyses presented here for the FLK Zinj assemblage lend support to recent interpretations by Domínguez-Rodrigo and colleagues (2007a) of hominin and carnivore activities at this site and are consistent with a scenario of hunting or aggressive scavenging from felid kills. From a comparative taphonomic examination of faunal assemblages from these two sites, the following conclusions can be drawn:

1. Frequencies of hominin-induced modifications are higher at FLK Zinj than at Kanjera, and patterns of cut marks illustrated in GIS analyses indicate early access to fleshed carcasses, not

marginal scavenging.

2. Frequencies of carnivore-induced modifications as well as the intensity of tooth marking (indicated by higher degree of tooth mark clustering) identified in GIS analyses are higher at FLK Zinj than at Kanjera. Overall tooth marking frequencies at both sites, however, are low and are comparable to experimental models where hominins had primary access to carcasses. Tooth marking frequencies reported here are lower than those originally reported by Blumenschine (1995) and are inconsistent with a passive scavenging model of meat acquisition for hominins. Tooth mark frequencies are concordant with those reported by Domínguez-Rodrigo et al. (2007a).

3. Bone fragmentation levels are high at both FLK Zinj and Kanjera and resemble experimental scenarios where hominins had primary access and engaged in marrow extraction, not carnivore accumulated assemblages. The GIS experimental models of skeletal part profiles for carnivore scavenging are not robust enough to be conclusive, but the overall bone portion survivorship at Zinj and Kanjera is generally higher than in experimental models where hyenas scavenged bones butchered by humans. This may indicate lower carnivore involvement / lower competition at Zinj and Kanjera than has been modeled experimentally.

4. Similarity in the “early access” signal at Kanjera and FLK Zinj, but differing levels of bone surface damage, may indicate behavioral differences in hominins at these sites or may be related to different competitive regimes in the paleoecosystems at these sites.

5. The relatively complete small bovid remains at Kanjera are likely to have been acquired through hunting. Active scavenging is not likely to explain hominin acquisition of relatively

complete small bovids, as hyenas tend to completely destroy small carcasses (although felids and canids do not – see Chapters 1-2). The small bovid mortality profile dominated by young individuals suggests a likely scenario of persistence hunting by hominins to obtain these carcasses. Larger bovids are rarer in the Kanjera assemblage, and so their mode of acquisition by hominins is more difficult to interpret, but my data are not inconsistent with Ferraro et al.'s (2013) interpretation of a selective scavenging strategy, whereby limb elements and heads were specifically chosen and transported to Kanjera for their within bone tissues. Early access to smaller carcasses by hominins at FLK Zinj was also likely to have been achieved through hunting. For the larger bovids at FLK Zinj, hunting cannot be ruled out, but aggressive scavenging of large bovids from felids seems to equally or more plausibly explain early hominin access. Some isolated bone damage traces that I have identified in the FLK Zinj assemblage are identical to those produced by large felids in my experimental studies (Chapter 4 Fig. 4.10). Bunn and Pickering (2010) have argued that the prime-dominated bovid mortality profile at FLK Zinj does not match that for modern lions. However, the greater diversity of large felids in Plio-Pleistocene times with presumably differing feeding niches may also have created differing prey mortality profiles. The bovid mortality profile in the Olduvai background scatter, which is largely attributed to extinct felid predation (see Domínguez-Rodrigo et al. 2007a), closely resembles the FLK Zinj large bovid mortality profile. This suggests that hominins at FLK Zinj could have actively scavenged large bovids from kills of extinct sabertooth felids.

Evolutionary Implications for Hominin Early Access to Carcasses

The archaeofaunal assemblage from Kanjera South provides the earliest evidence for persistent hominin carnivory in the archaeological record and perhaps the earliest evidence for hunting. Prior to 2 Ma, isolated occurrences of cut marked bone are found at the Ethiopian sites of Gona, (2.6 Ma; Semaw et al. 2003), Bouri (2.5 Ma; de Heinzelin et al. 1999), and more controversial evidence comes from Dikika at ca. 3.4 Ma (McPherron et al. 2010; Domínguez-Rodrigo et al. 2010). However, none of these early sites document hominin involvement on the scale that is seen after 2 Ma at Kanjera and FLK Zinj, as well as at other Oldowan sites including DK, Olduvai Gorge (Potts 1988; Domínguez-Rodrigo 2007a); FwJj20, Koobi Fora (McCoy 2009; Braun et al. 2010); and other sites in East Turkana, Kenya (Pobiner et al. 2008).

This evidence for a dietary shift to include a greater amount of animal tissue in the diet occurs at a critical time in hominin evolution and is roughly associated with the first appearance of the genus *Homo* (2.33 Ma; Kimbel et al. 1996). Morphological changes in the hominin lineage from *Australopithecus* to early *Homo* include a significant increase in brain size and a shift toward longer limbs and modern body proportions. These features are well-established by the time *Homo erectus* appears (Anton 2003; Haeusler and McHenry 2004). Brains are metabolically expensive organs, and an increase in brain size would also have entailed an increased nutritional requirement for early *Homo* (Aiello and Wheeler 1995). As a nutritionally-dense resource providing protein, fat, and many essential vitamins and minerals in an easily digestible form, it is likely that meat played a key role in fulfilling these requirements (Milton 1999). High quality dietary sources may have been particularly important to children. Due to their large brains, and high nutrient and energy demands, modern human children require foods of high nutritional value for growth and development This was also likely the case for the young of early *Homo*. Given the increase in brain size seen in early *Homo*, it is likely that meat would have been an important component in the diet of weaned *Homo habilis* and *Homo erectus* children (Plummer 2004).

The morphological changes seen in early *Homo* are thought to have been spurred by environmental change. A cooling and drying trend took place in Africa with the onset of glaciation in the northern hemisphere between 2.0-3.0 Ma. This trend resulted in an expansion grasslands relative to forest habitats (deMenocal 1995; Wynn 2004; Bobe 2006). Evidence for the expansion of grasslands was the basis of the influential "savanna hypothesis," which held that spread of dry, open grassland habitats provided the selective pressure for the development of a suite of unique hominin adaptations (Vrba 1985, 1995). Potts (1998, 2012, 2013) has suggested that an increase in climactic variability which led to resource instability during the Plio-Pleistocene may instead have been a driving force behind the dietary shift seen in early *Homo*. Potts has argued that increased habitat heterogeneity selected for adaptability in early *Homo* rather than adaptation to a specific environmental pressure. He argued that tools also may have developed at this time to serve as a buffer against habitat instability by providing access to new food items and allowing for dietary expansion.

The dietary and morphological changes seen in early *Homo* also suggest a change in hominin socioecology. The development of longer limbs beginning with earliest genus *Homo* suggests the potential for increased ranging behavior (Haeusler and McHenry 2004). More dispersed food resources in savanna environments as well as a greater likelihood for competition with large carnivores may have promoted group cohesion, cooperation in foraging, and transport of food resources to safe areas by hominins (Oliver 1994; Rose and Marshall 1996; Lewis 1997; Plummer 2004). These behaviors may have created a context for the development of food-sharing, the importance of which was originally suggested by Isaac (1978, 1983) in his "home base" (later "central place") hypothesis. While there is no evidence for a sexual division of labor in foraging behavior as assumed by Isaac's "home base" model, the greater nutritional requirements indicated for the young of early *Homo* would have meant that females could have increased their reproductive success if they were part of a support network that included provisioning or help from others. Provisioning may have come from males or female relatives (Hawkes et al. 1998; O'Connell et al. 1999; Rose 2001; Aiello and Key 2002; Plummer 2004; Panter-Brick 2002). This scenario may have laid the groundwork for development of the widespread food sharing which is seen in modern humans (Kaplan and Hill 1985; Hawkes et al. 2001; Marlowe 2001). The data indicating early access to carcasses at Kanjera South adds one piece of evidence to our understanding hominin dietary evolution within this broader context.

BENEFITS OF THE GIS IMAGE ANALYSIS METHODOLOGY AND DIRECTIONS FOR FUTURE RESEARCH

The use of the GIS image analysis method and my expansion on this method to include ArcGIS Spatial Analyst tools provides a valuable means of visually characterizing large sets of neotaphonomic data which can be used to interpret fossil assemblages. This methodology adds a new dimension to the study of hominin and carnivore feeding traces in archaeofaunal assemblages.

This work presented here has only focused on bone damage patterns at two sites, but applying this methodology to other Early Pleistocene assemblages could help to increase our understanding of hominin-carnivore competition during this period. Of particular interest are some of the other Bed I sites at Olduvai. Domínguez-Rodrigo and colleagues (2007a, 2009) have argued that most of the assemblages at FLK North and FLK North North, which were originally identified by Leakey (1971) as hominin "living floors," actually represent "palimpsests" of unrelated hominin and carnivore activities at the site. Part of this argument is based on the lack of associated stone tools with the faunal assemblages. Another part of the argument is that gross bone damage in these assemblages shows hallmark characteristics of felid modification. The felid experimental model Domínguez-Rodrigo et al. (2007a) applied to interpret these assemblages was based only on a small assemblage of mostly leopard-modified bones from experiments conducted by Brain (1981) which had a sample size of 6 small bovids, a baboon, and a cow (described in Domínguez-Rodrigo et al. 2007b). The experimental work presented in this dissertation adds a much larger sample size of felid-modified bones and provides a stronger experimentally-based backing to the pattern of bone damage produced by felids that Domínguez-Rodrigo and colleagues identified. Future analysis of these FLK N assemblages using GIS image analysis may help to evaluate his hypothesis.

Another avenue of future research which naturally extends from the work presented here is the necessity to increase the available neotaphonomic assemblages modeling dual-patterned sites. The number assemblages modeling carnivore scavenging of human butchered bones needs to be increased, but also, virtually no work has been done to model hominin scavenging from carnivore kills (but see Domínguez-Rodrigo 2007b). Additional feeding experiments with hyaenids would help to strengthen models of their bone damage signal. Also, GIS modeling of actual archaeofaunal assemblages known to have been modified by carnivores in the past (e.g., *Homotherium* assemblage from Friesenhahn Cave, Texas) would help to address questions regarding the reliability of using modern carnivore bone damage patterns as proxies for extinct carnivore capabilities. Because accurate interpretation of fossil assemblages depends on the robusticity of our experimental models, we should strive to include as many relevant variables as possible in these models, to ensure they are comprehensive enough to reliably test hypotheses about hominin behaviors in the past.

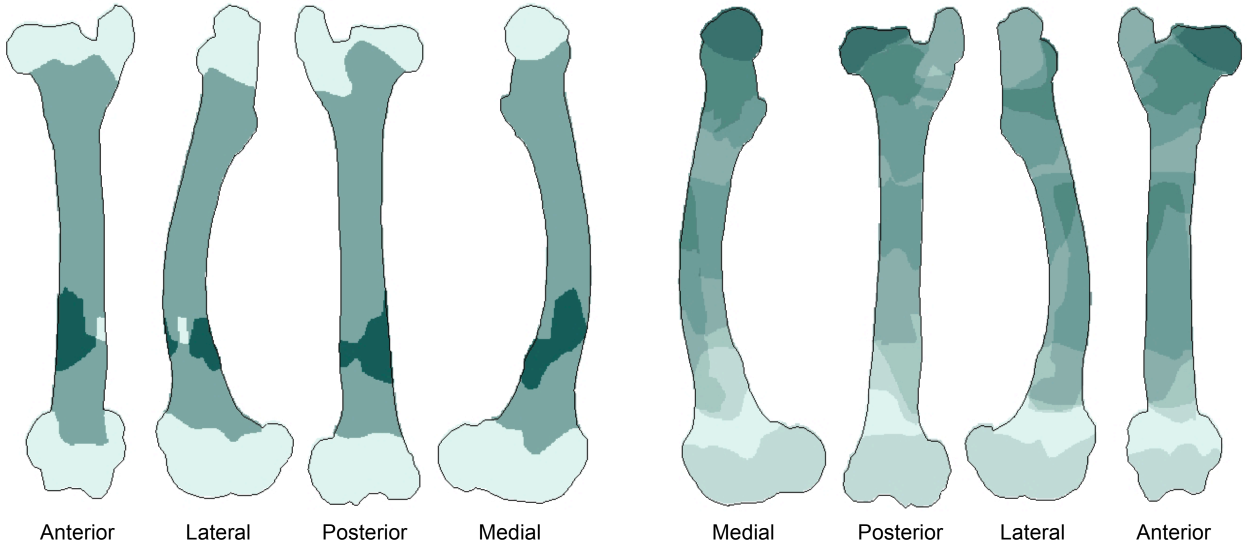
APPENDIX A

FIGURES DISPLAYING BONE PRESERVATON PATTERNS IN THE KANJERA SOUTH ASSEMBLAGE AND IN EXPERIMENTAL ASSEMBLAGES REFERRED TO IN TEXT

Figure A.1. Preservation of the femora at Kanjera (small and medium bovids)
Small bovids = size class 1, medium bovids = size class 2-3a. n = minimum number of elements estimate (greatest number of overlapping fragments; note n ≠ the NISP for each model).

Kanjera Small Bovids (Left Side)
n = 3

Kanjera Small Bovids (Right Side)
n = 7



Kanjera Medium Bovids (Left Side)
n = 8

Kanjera Medium Bovids (Right Side)
n = 6

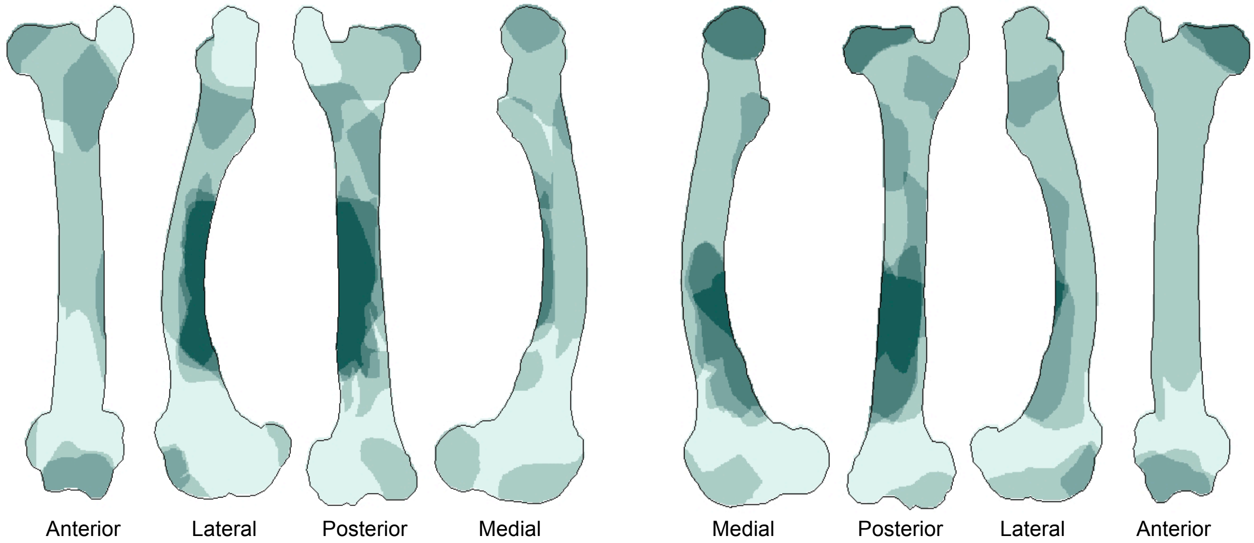
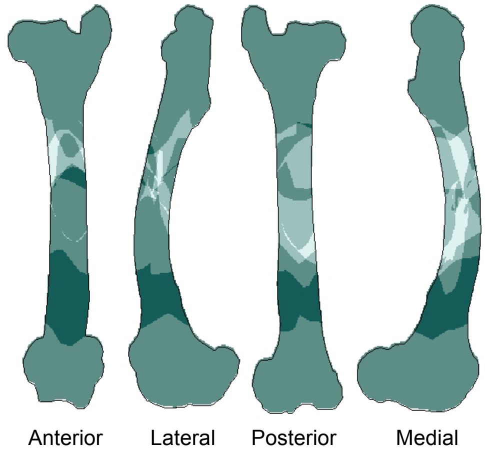
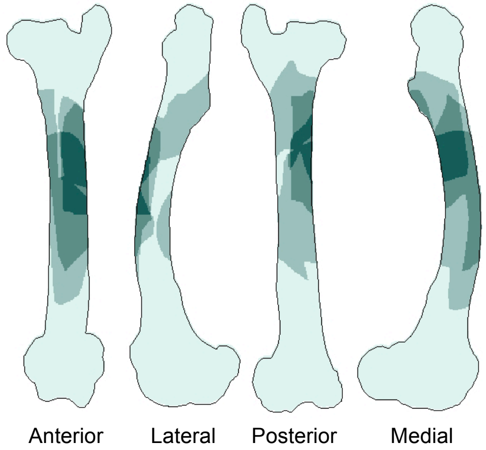


Figure A.2. Preservation of the femora in experimental assemblages (small and medium bovids combined). Hammerstone Only, Hammerstone → Carnivore, and Hyaenid assemblages are from Blumenschine's experiments, and represent right/left composite images shown on a left side template. Felid and Canid experiments are from this study (Chapters 1 & 2).

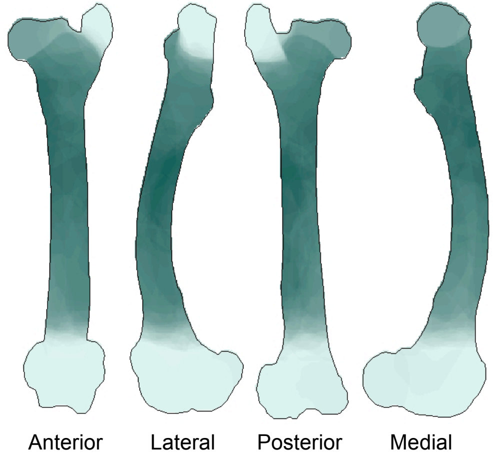
Hammerstone Only n = 8



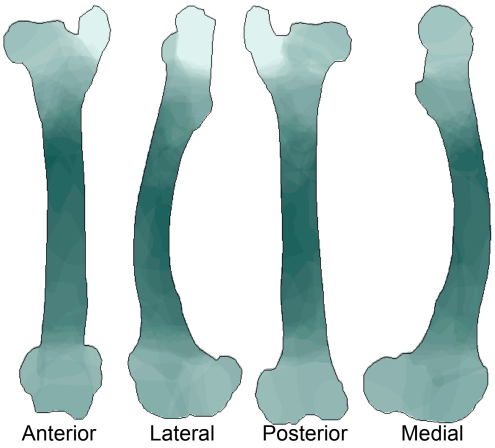
Hammerstone → Carnivore n = 4



Carnivore Only – Felid n = 48



Carnivore Only – Canid n = 50



Carnivore Only – Hyaenid n = 1

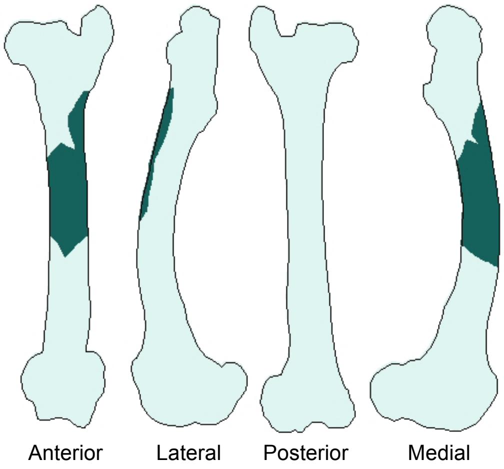
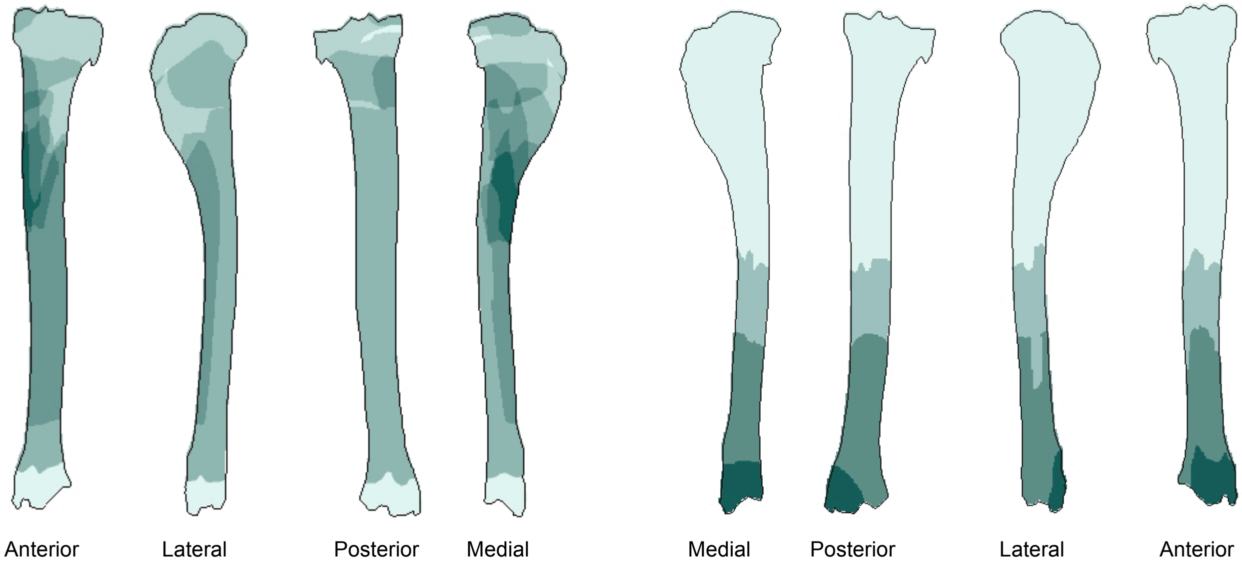


Figure A.3. Preservation of the tibiae at Kanjera (small and medium bovids). See Fig. A.1 caption for details.

Kanjera Small Bovids (Left Side)
n = 5

Kanjera Small Bovids (Right Side)
n = 3



Kanjera Medium Bovids (Left Side)
n = 8

Kanjera Medium Bovids (Right Side)
n = 9

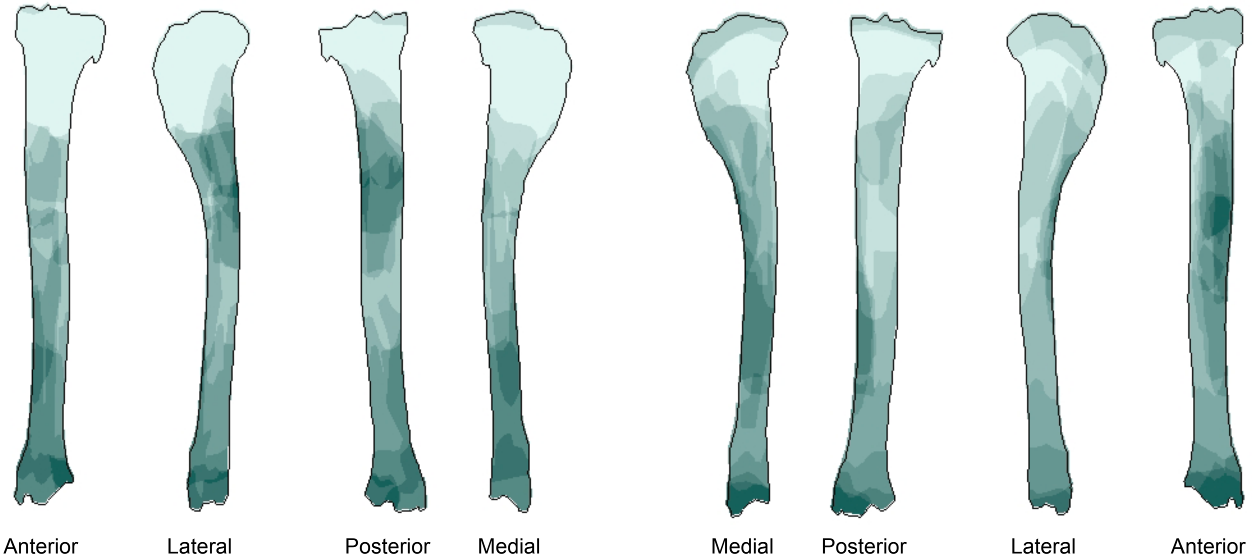
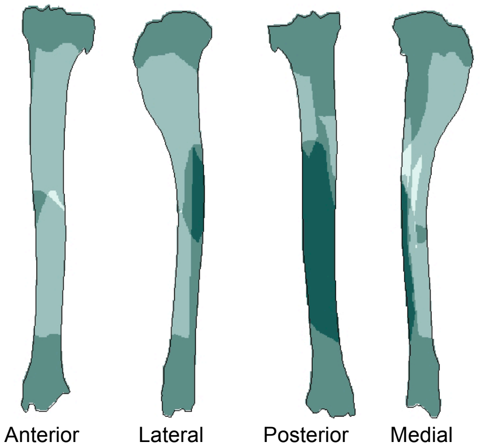
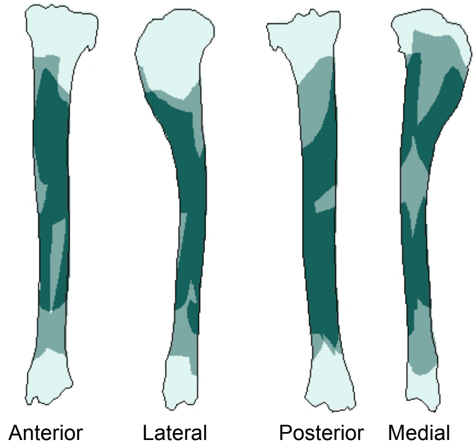
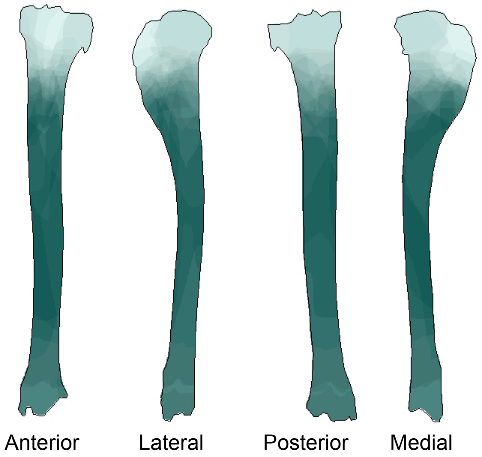
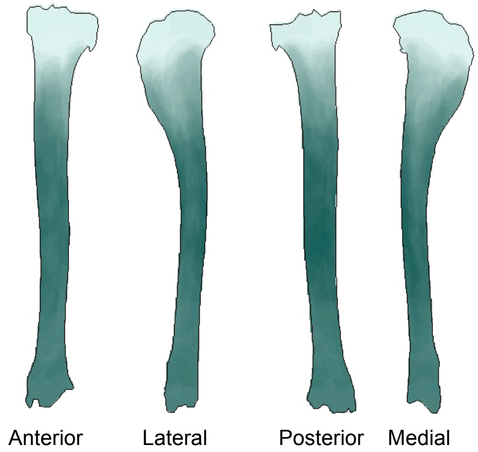


Figure A.4. Preservation of the tibiae in experimental assemblages (small and medium bovids combined). See Fig. A.2 caption for details.


Hammerstone Only n = 6


Hammerstone → Carnivore n = 2


Carnivore Only – Felid n = 52


Carnivore Only – Canid n = 62

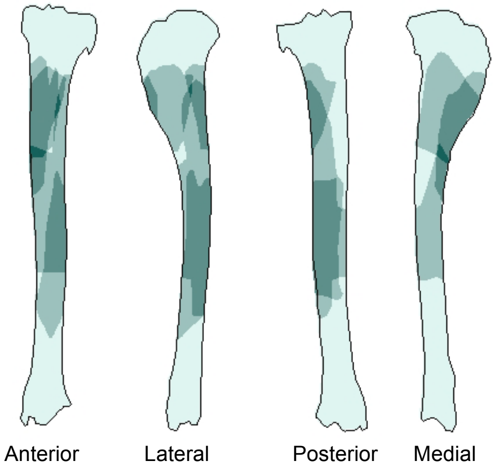
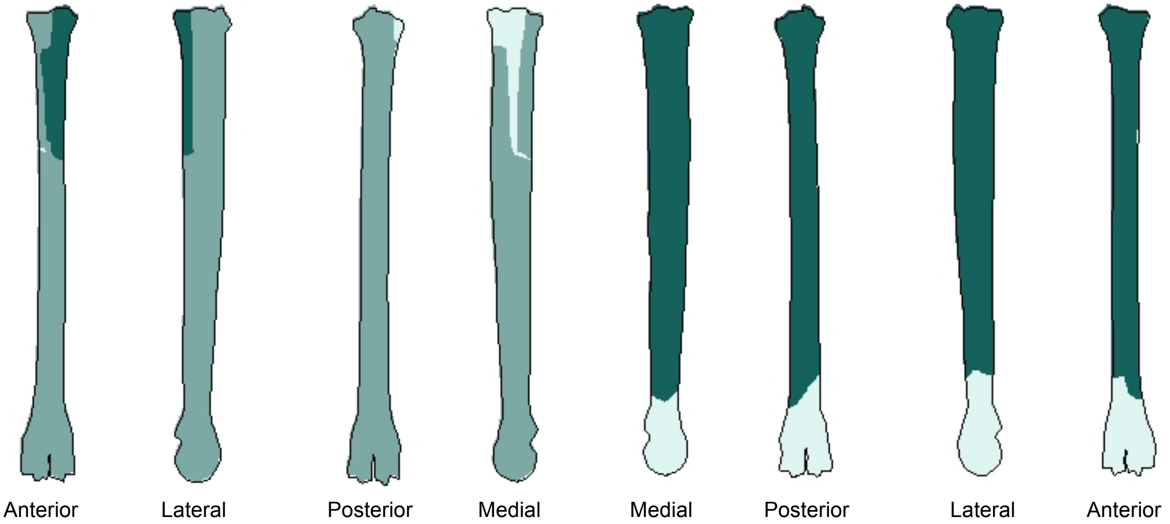
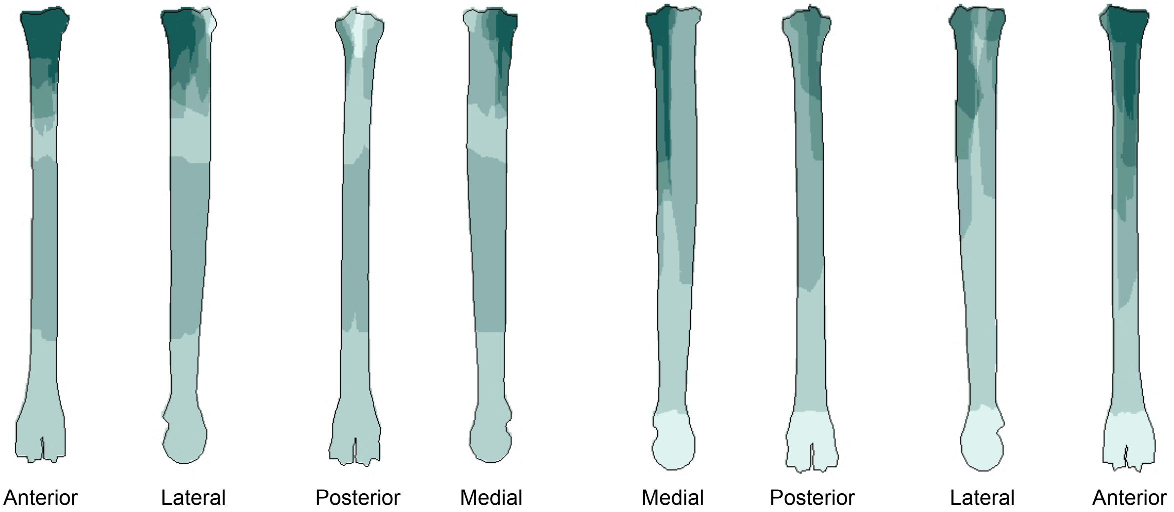

Carnivore Only – Hyaenid n = 3

Figure A.5. Preservation of the metatarsals at Kanjera (small and medium bovids). See Fig. A.1 caption for details.



Kanjera Small Bovids (Left Side)
n = 3

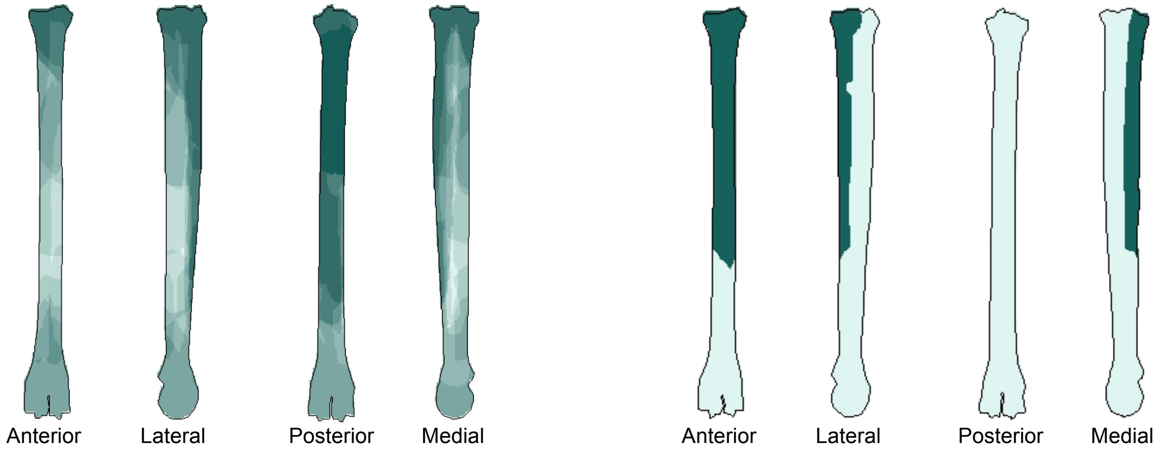
Kanjera Small Bovids (Right Side)
n = 2



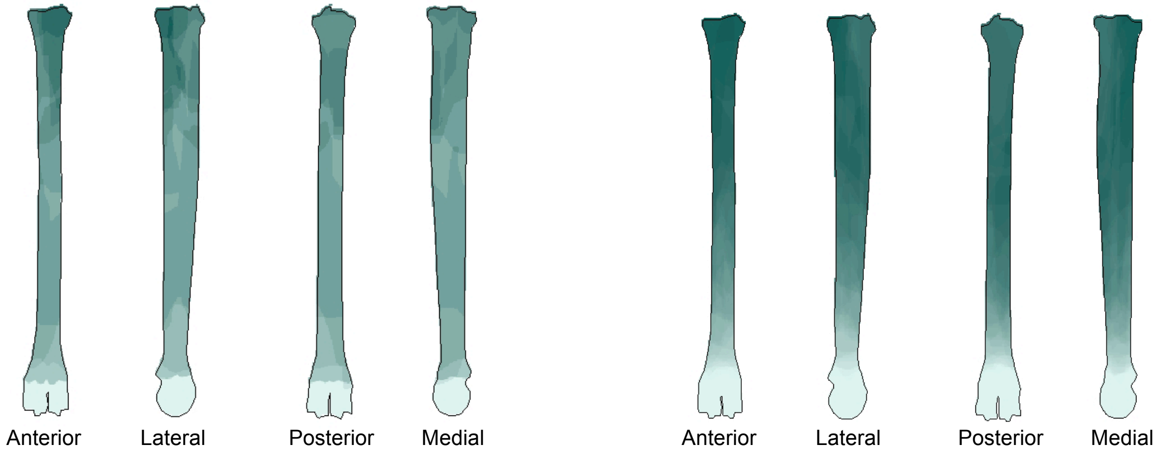
Kanjera Medium Bovids (Left Side)
n = 7

Kanjera Medium Bovids (Right Side)
n = 6

Figure A.6. Preservation of the metatarsals in experimental assemblages (small and medium bovids combined). See Fig. A.2 caption for details.


Hammerstone Only n = 11

Hammerstone → Carnivore n = 1


Carnivore Only – Felid n = 38

Carnivore Only – Canid n = 47

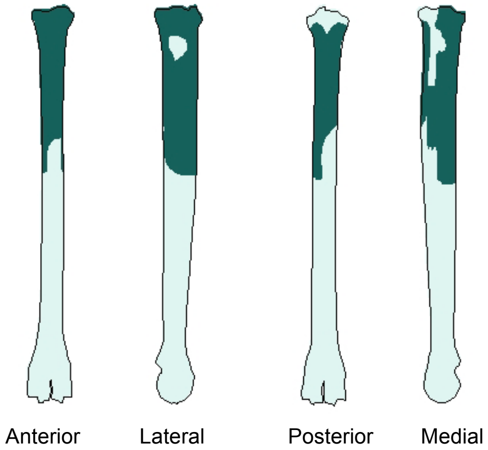
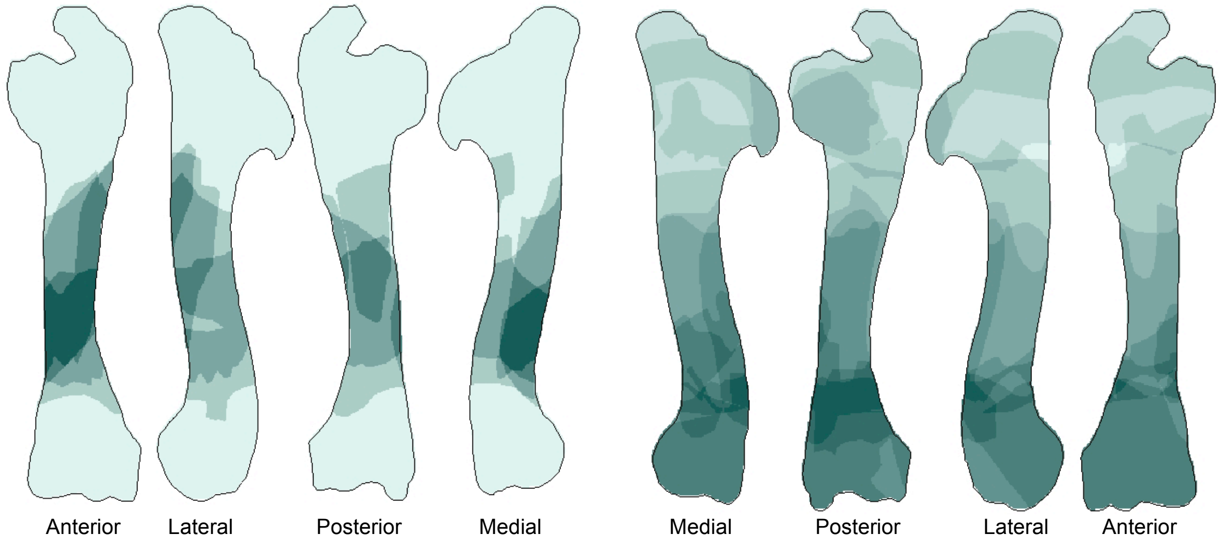

Carnivore Only – Hyaenid n = 1

Figure A.7. Preservation of the humeri at Kanjera (small and medium bovids). See Fig. A.1 caption for details.

Kanjera Small Bovids (Left Side)
n = 4

Kanjera Small Bovids (Right Side)
n = 9



Kanjera Medium Bovids (Left Side)
n = 9

Kanjera Medium Bovids (Right Side)
n = 15

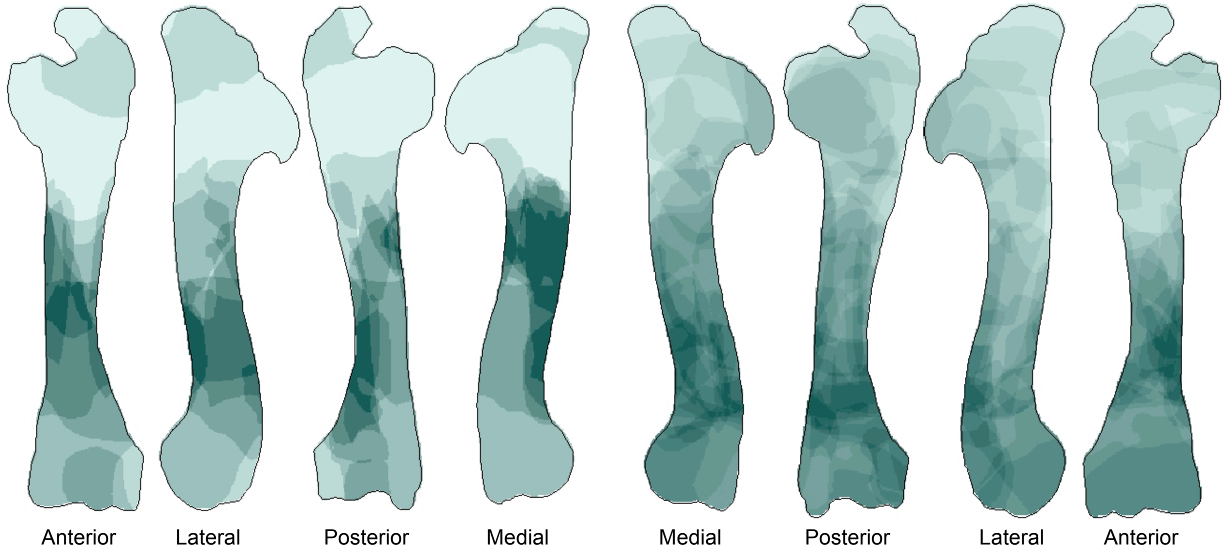
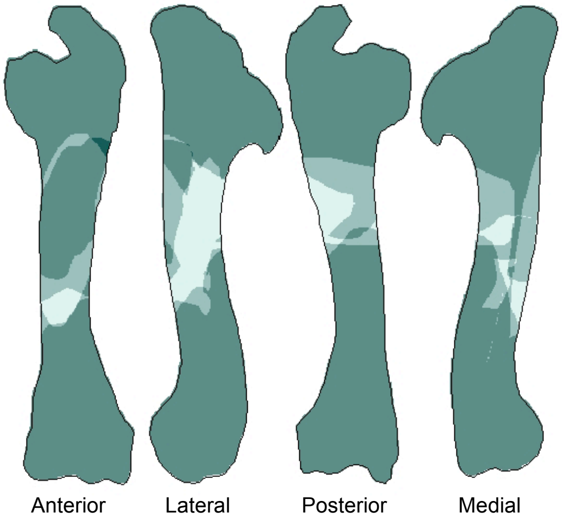
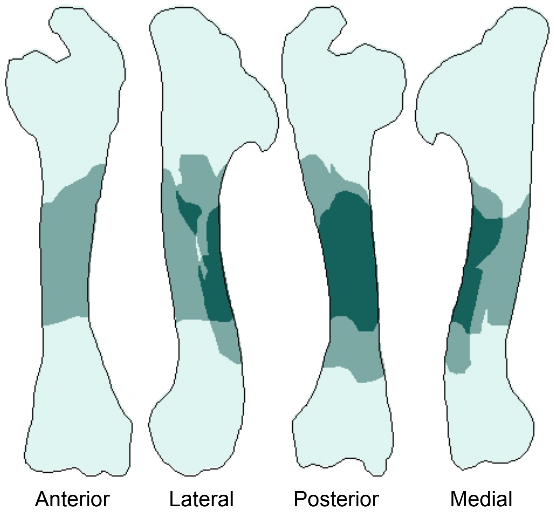


Figure A.8. Preservation of the humeri in experimental assemblages (small and medium bovids combined). See Fig. A.2 caption for details.

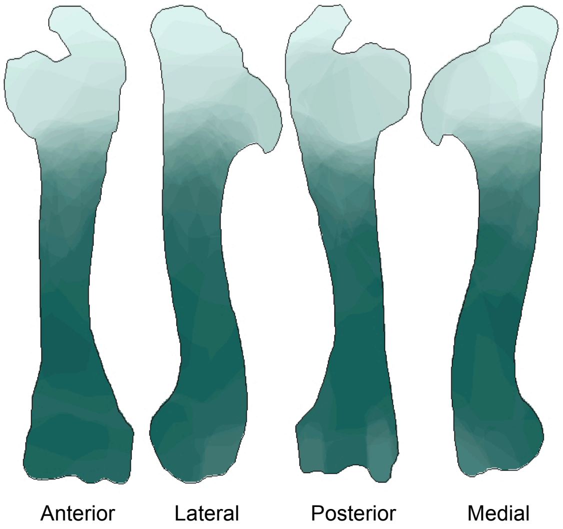
Hammerstone Only n = 7



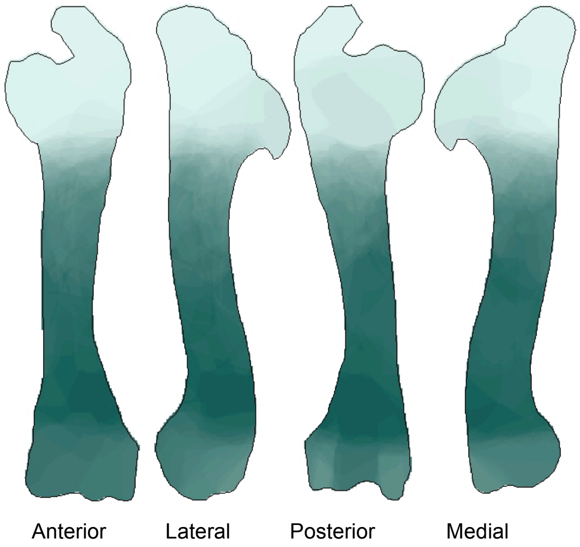
Hammerstone → Carnivore n = 3



Carnivore Only – Felid n = 56



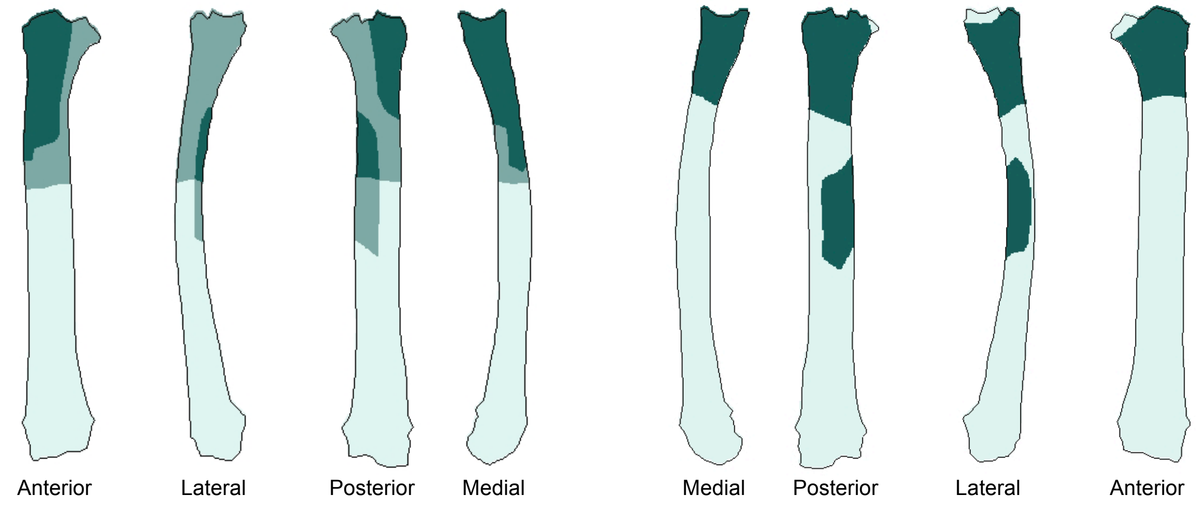
Carnivore Only – Canid n = 57



Carnivore Only – Hyaenid

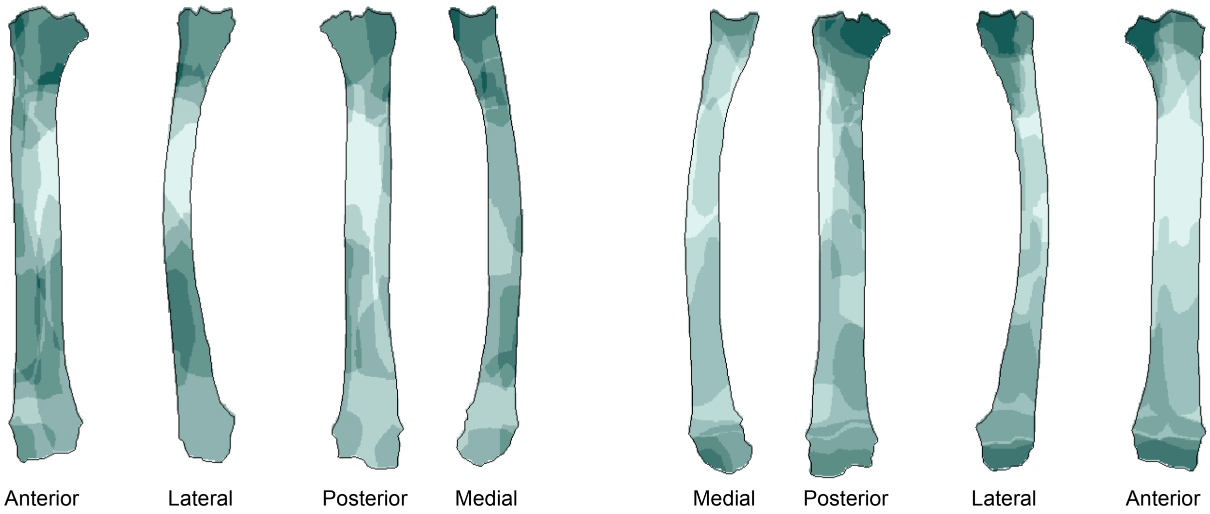
N/A

Figure A.9. Preservation of the radii at Kanjera (small and medium bovids). See Fig. A.1 caption for details.



Kanjera Small Bovids (Left Side)
n = 2

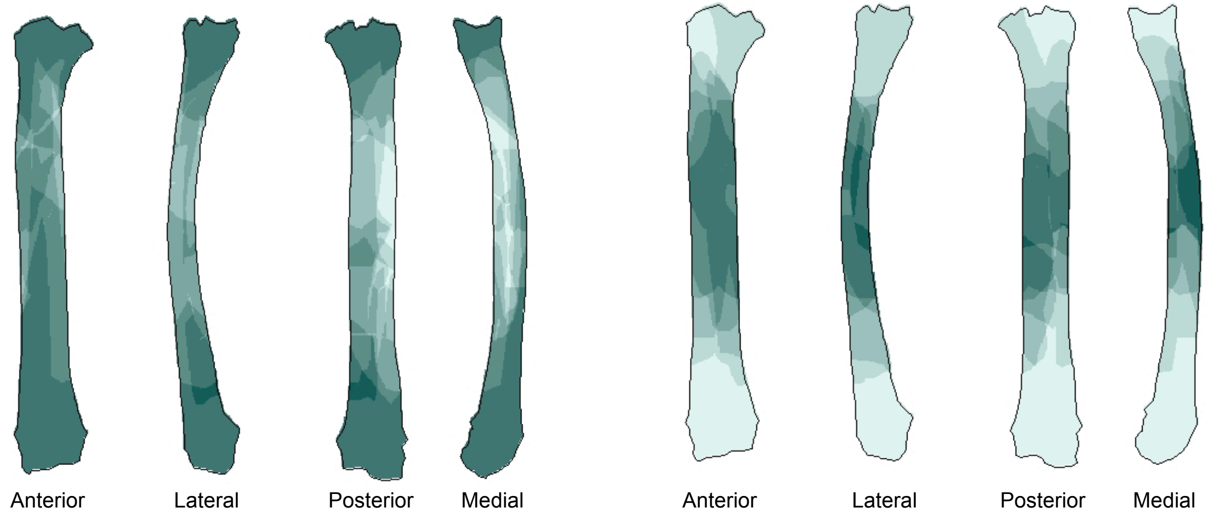
Kanjera Small Bovids (Right Side)
n = 2



Kanjera Medium Bovids (Left Side)
n = 6

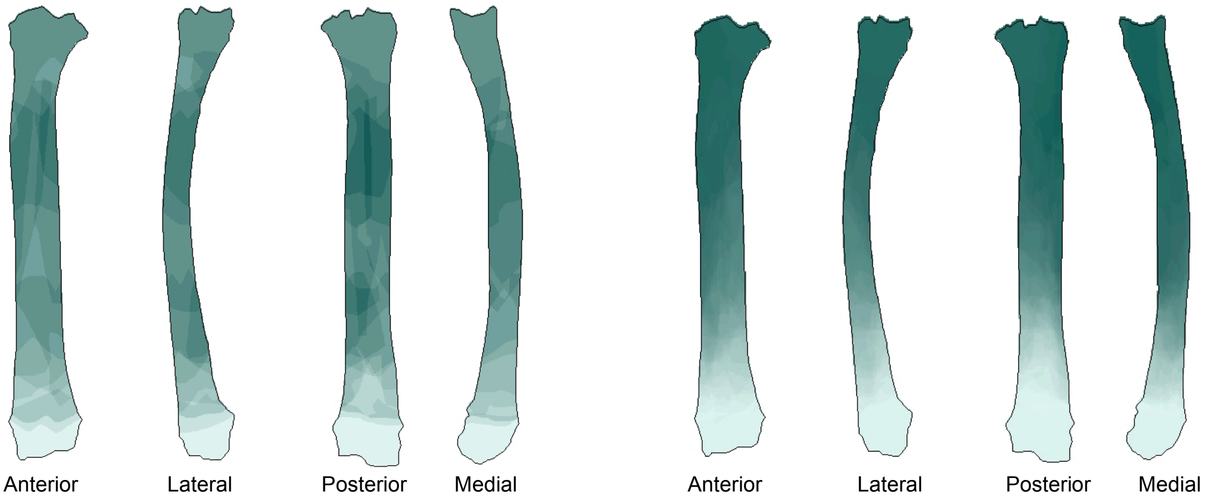
Kanjera Medium Bovids (Right Side)
n = 9

Figure A.10. Preservation of the radii in experimental assemblages (small and medium bovids combined). See Fig. A.2 caption for details.



Hammerstone Only n = 11

Hammerstone → Carnivore n = 6



Carnivore Only – Felid n = 57

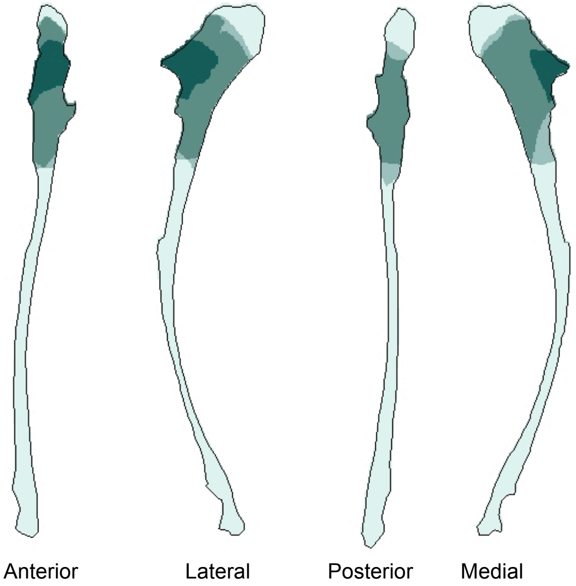
Carnivore Only – Canid n = 62

Carnivore Only – Hyaenid

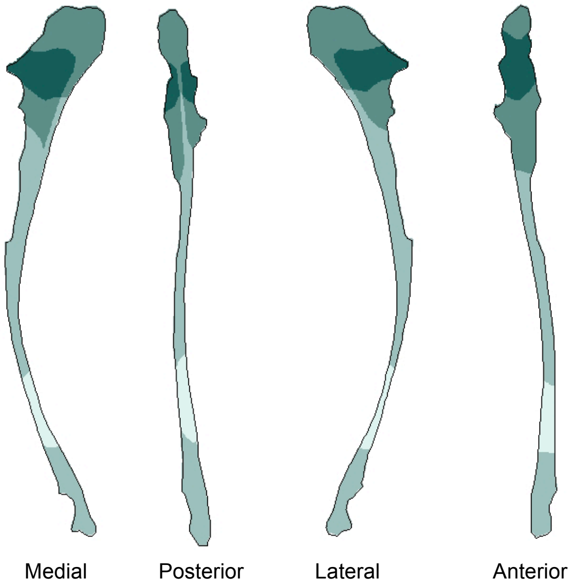
N/A

Figure A.11. Preservation of the ulnae at Kanjera (small and medium bovids). See Fig. A.1 caption for details.

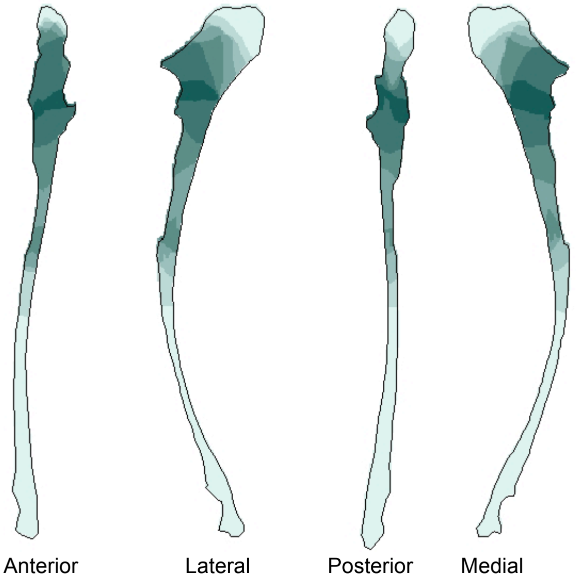
Kanjera Small Bovids (Left Side)
n = 3



Kanjera Small Bovids (Right Side)
n = 3



Kanjera Medium Bovids (Left Side)
n = 6



Kanjera Medium Bovids (Right Side)
n = 3

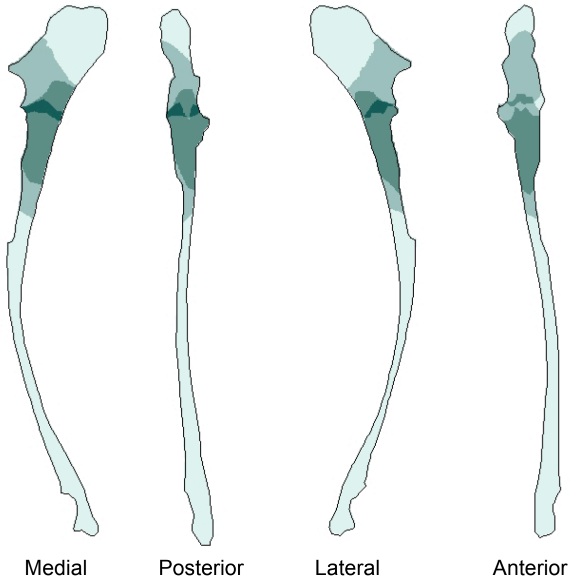
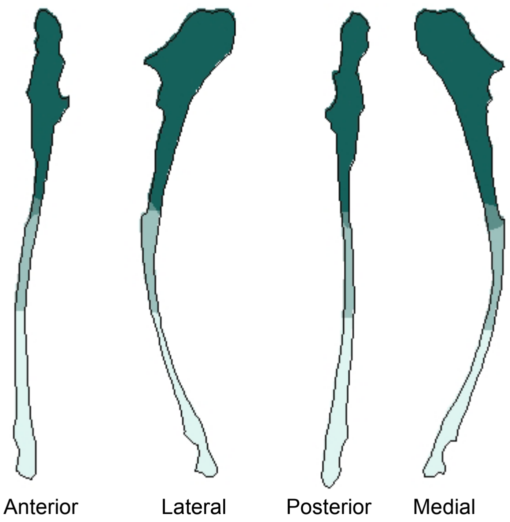
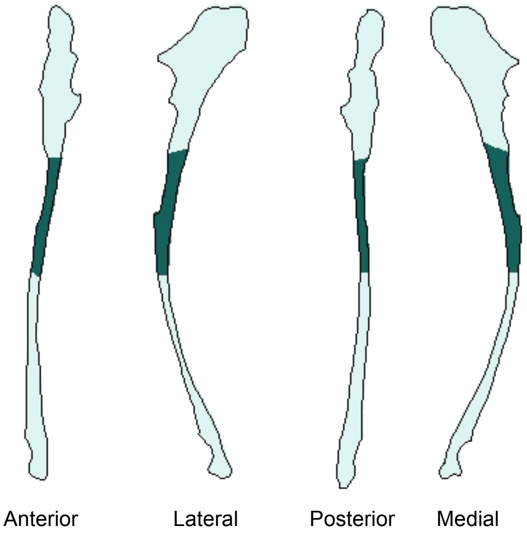


Figure A.12. Preservation of the ulnae in experimental assemblages (small and medium bovids). See Fig. A.2 caption for details.

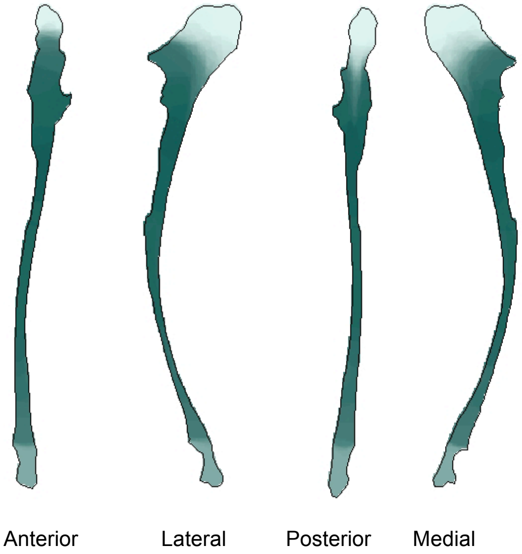
Hammerstone Only n = 8



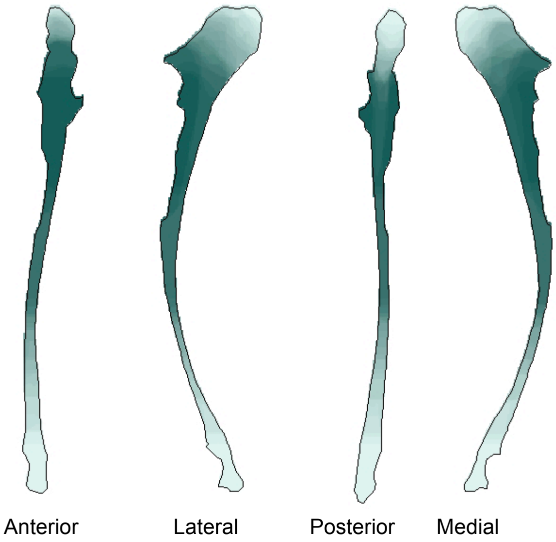
Hammerstone → Carnivore n = 1



Carnivore Only – Felid n = 55



Carnivore Only – Canid n = 32



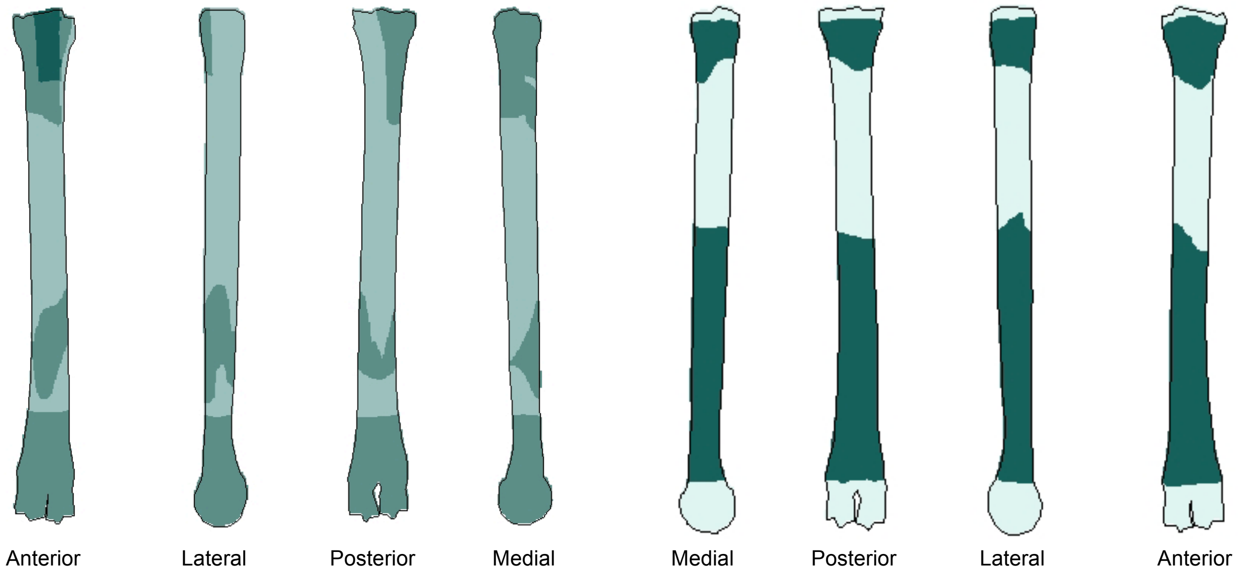
Carnivore Only – Hyaenid

N/A

Figure A.13. Preservation of the metacarpals at Kanjera (small and medium bovids). See Fig. A.1 caption for details.

Kanjera Small Bovids (Left Side)
n = 4

Kanjera Small Bovids (Right Side)
n = 1



Kanjera Medium Bovids (Left Side)
n = 8

Kanjera Medium Bovids (Right Side)
n = 6

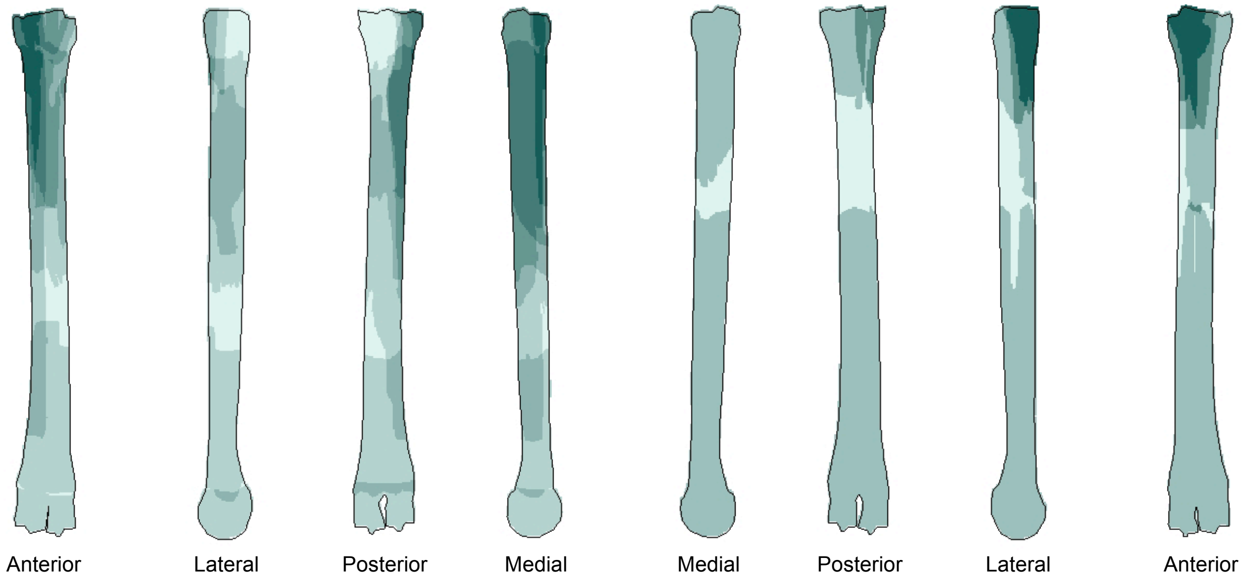
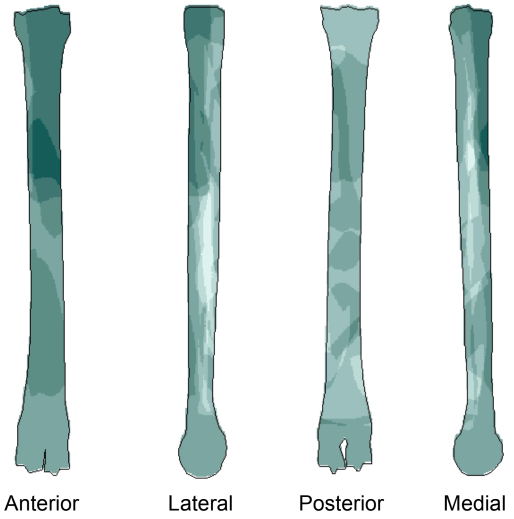
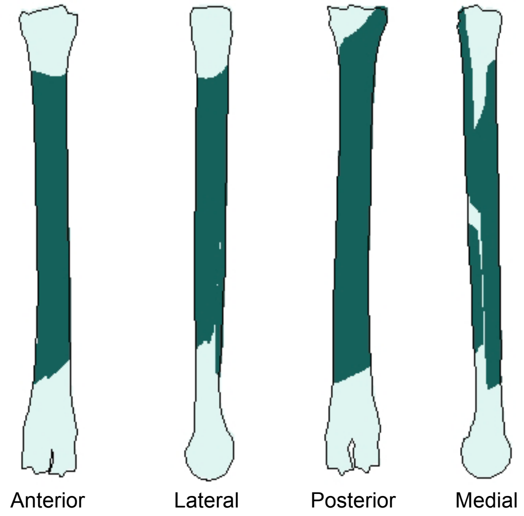


Figure A.14. Preservation of the metacarpals in experimental assemblages (small and medium bovids). See Fig. A.2 caption for details.

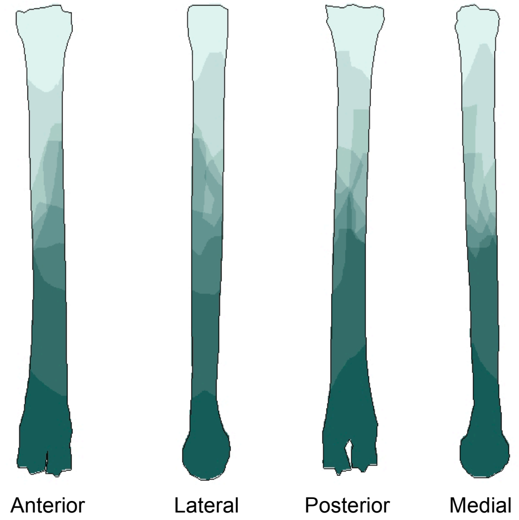
Hammerstone Only n = 10



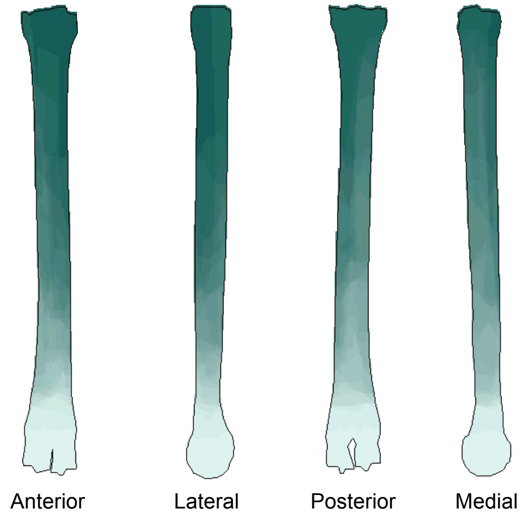
Hammerstone → Carnivore n = 1



Carnivore Only – Felid n = 53



Carnivore Only – Canid n = 32

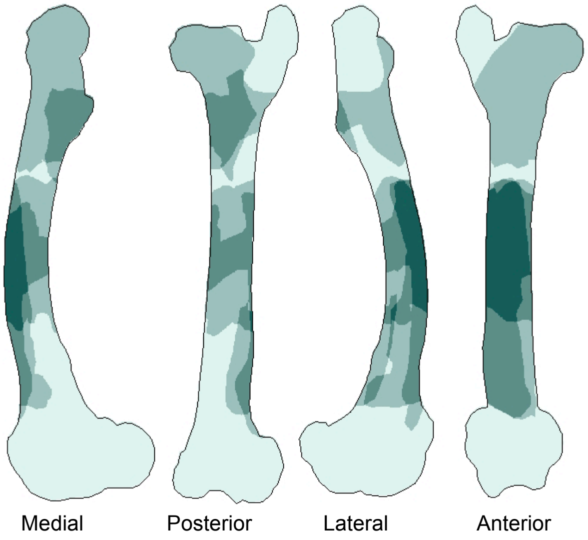


Carnivore Only – Hyaenid

N/A

Figure A.15. Preservation of the femora at Kanjera and in experimental models (large bovids, size 3b). Only the right side is present at Kanjera. Experimental assemblages represent right/left composite images shown on a left side template. Hammerstone only model not available for femora.

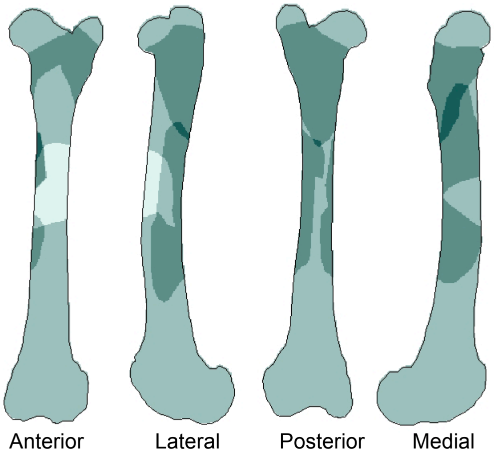
Kanjera Large Bovids (Right side) n = 3



Hammerstone Only

N/A

Hammerstone → Carnivore n = 3



Carnivore Only – Hyaenid n = 3

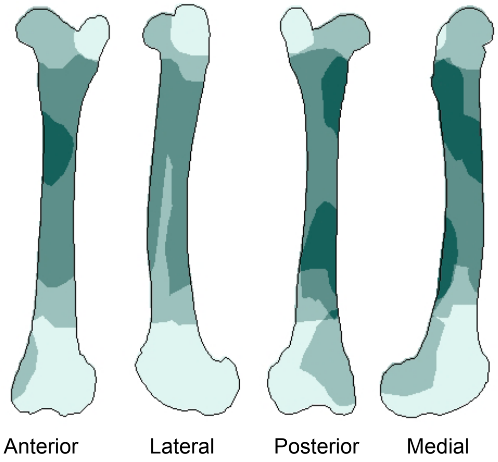
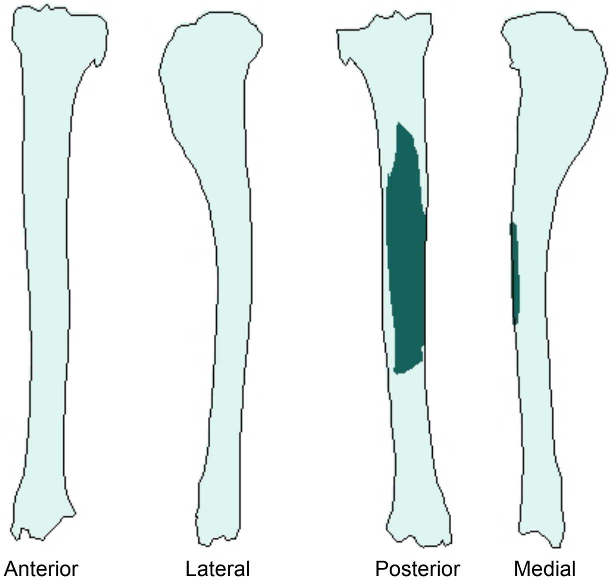


Figure A.16. Preservation of the tibiae at Kanjera and in experimental models (large bovids, size 3b). Only the left side is present at Kanjera. Experimental assemblages represent right/left composite images shown on a left side template. Hammerstone only model not available for tibiae.

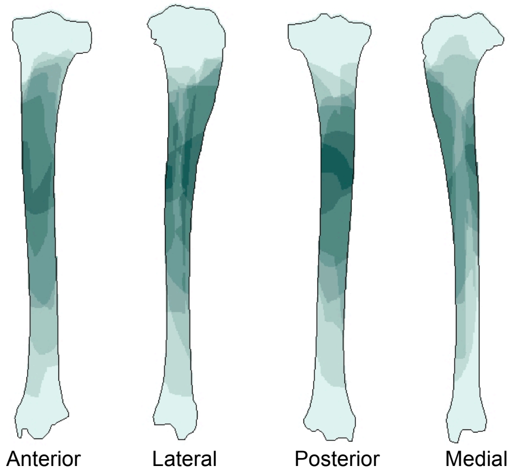
Kanjera Large Bovids (Left side) n = 1



Hammerstone Only

N/A

Hammerstone → Carnivore n = 7



Carnivore only – Hyaenid n = 6

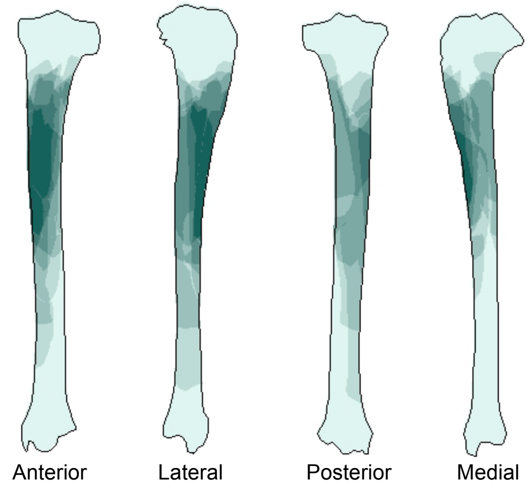


Figure A.17. Preservation of the metatarsals at Kanjera and in experimental models (large bovids, size 3b). Only the right side is present at Kanjera. Experimental assemblages represent right/left composite images shown on a left side template.

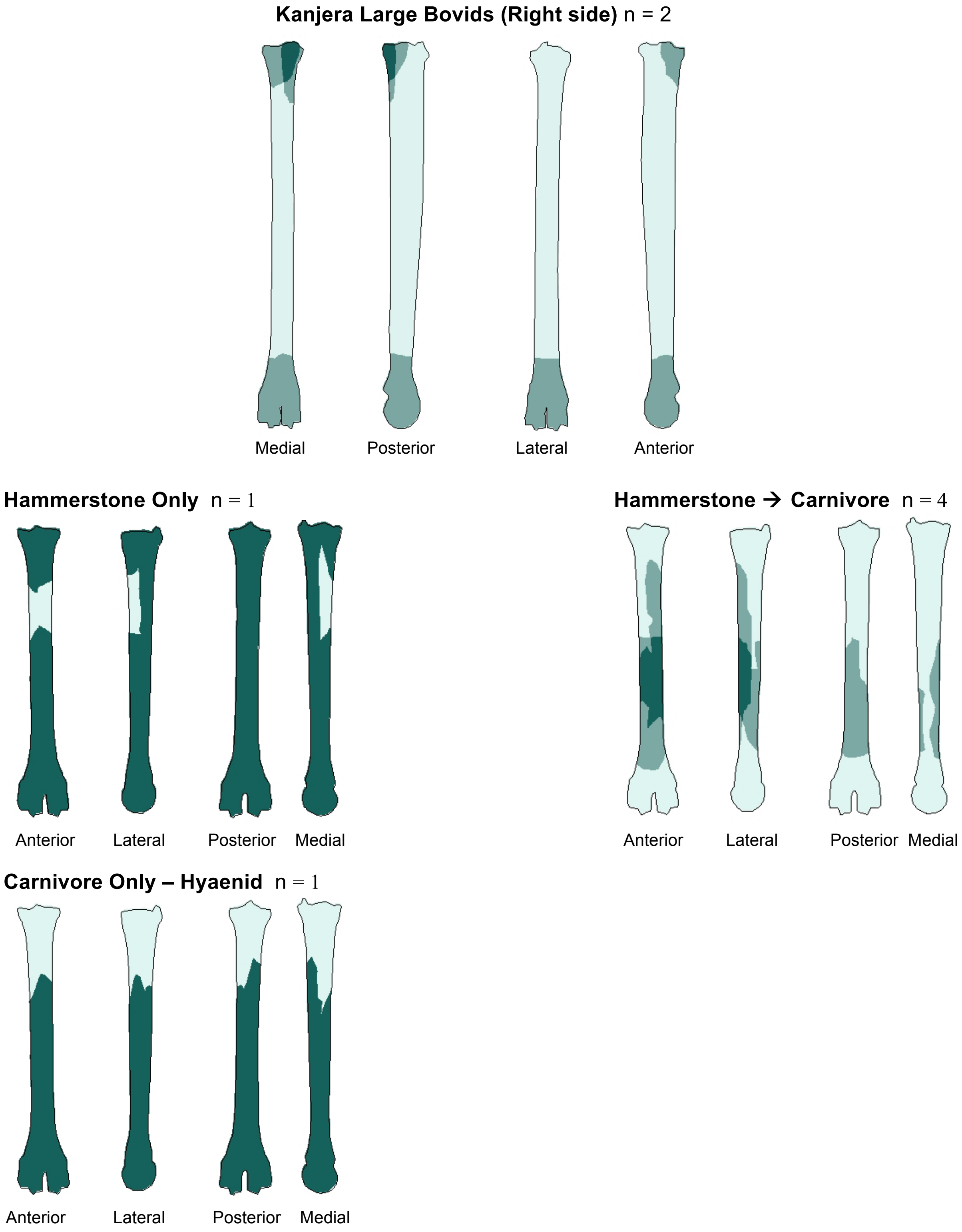
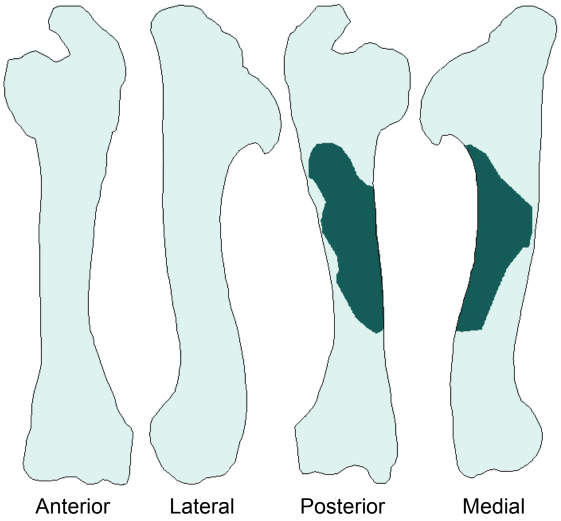
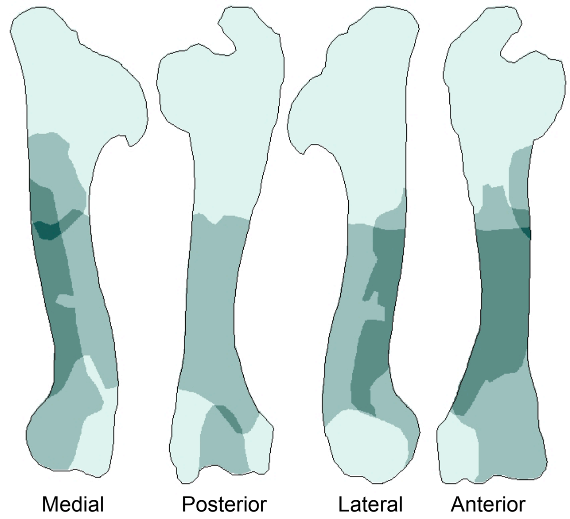


Figure A.18. Preservation of the humeri at Kanjera and in experimental models (large bovids, size 3b). Experimental assemblages represent right/left composite images shown on a left side template.

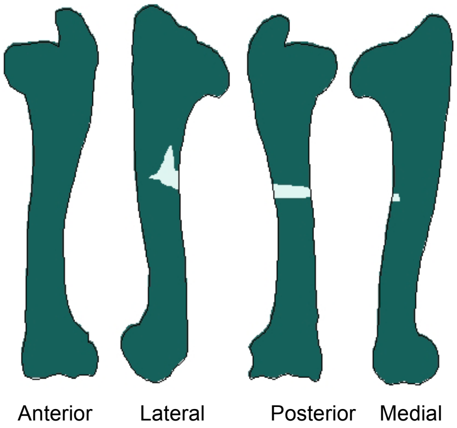
Kanjera Large Bovids (Left side) n = 1



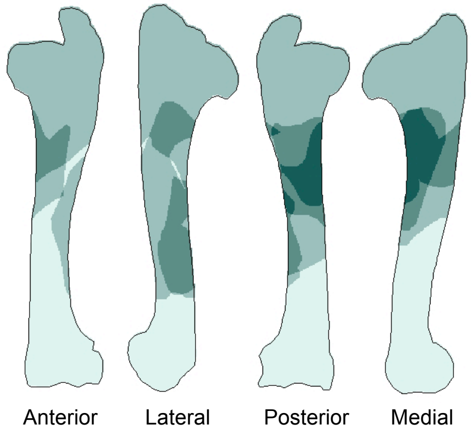
Kanjera Large Bovids (Right side) n = 3



Hammerstone Only n = 1



Hammerstone → Carnivore n = 3



Carnivore Only – Hyaenid n = 3

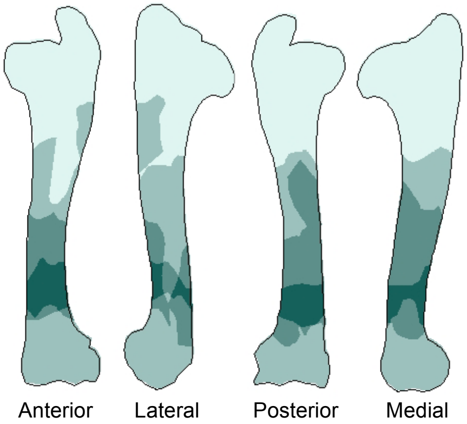
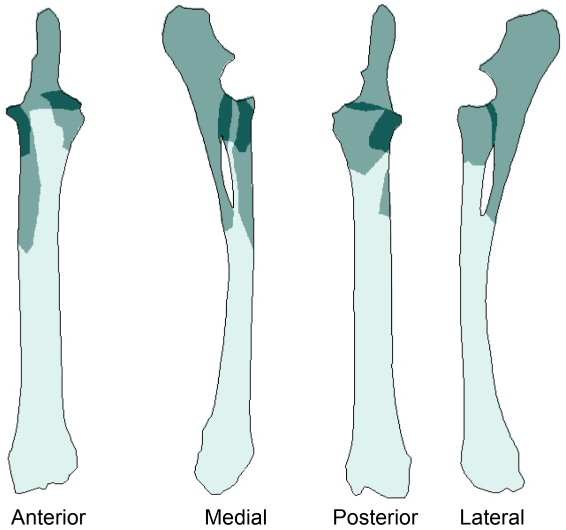
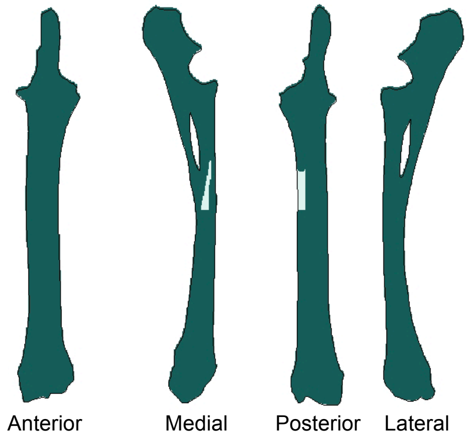


Figure A.19. Preservation of the radio-ulnae at Kanjera and in experimental models (large bovids, size 3b). Only the left side is present at Kanjera. Experimental assemblages represent right/left composite images shown on a left side template.

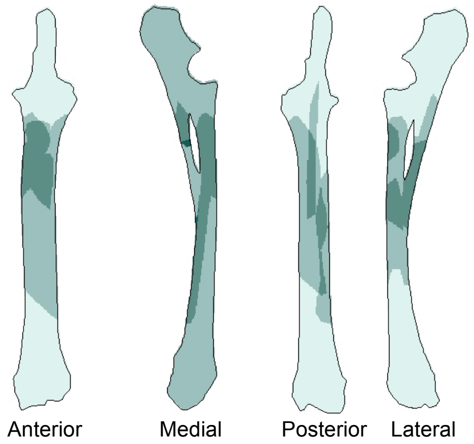
Kanjera Large Bovids (Left side) n = 2



Hammerstone Only n = 1



Hammerstone → Carnivore n = 3



Carnivore Only - Hyaenid n = 2

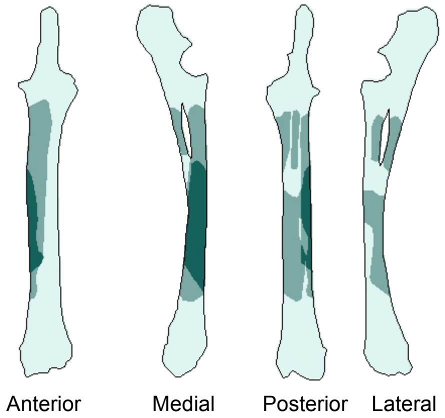
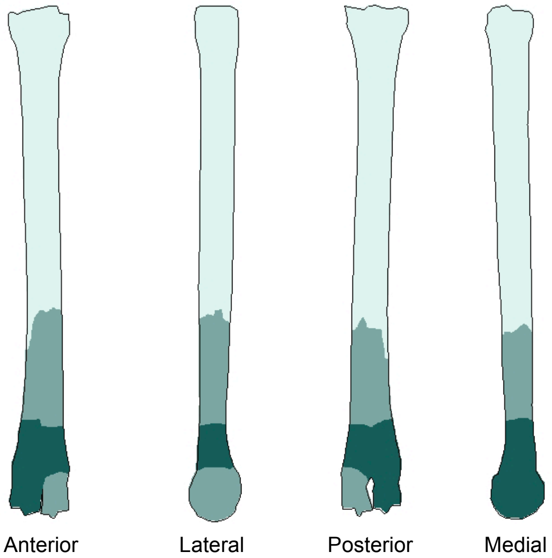
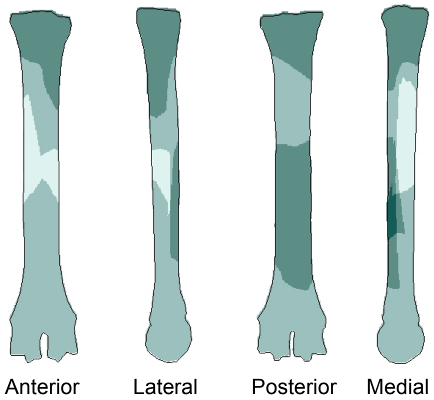


Figure A.20. Preservation of the metacarpals at Kanjera and in experimental models (large bovids, size 3b). Only the left side is present at Kanjera. Experimental assemblages represent right/left composite images shown on a left side template.

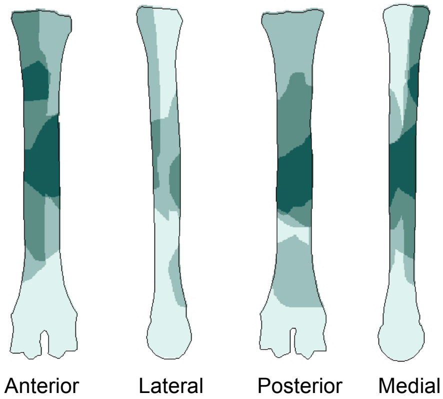
Kanjera Large Bovids (Left side) n = 2



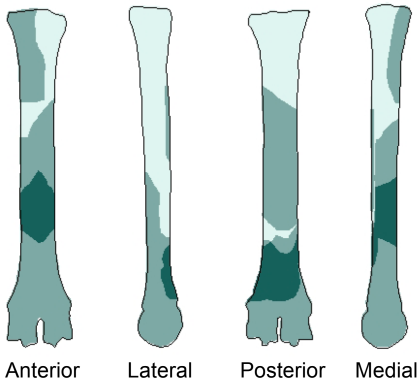
Hammerstone Only n = 3



Hammerstone → Carnivore n = 3



Carnivore Only – Hyaenid n = 2



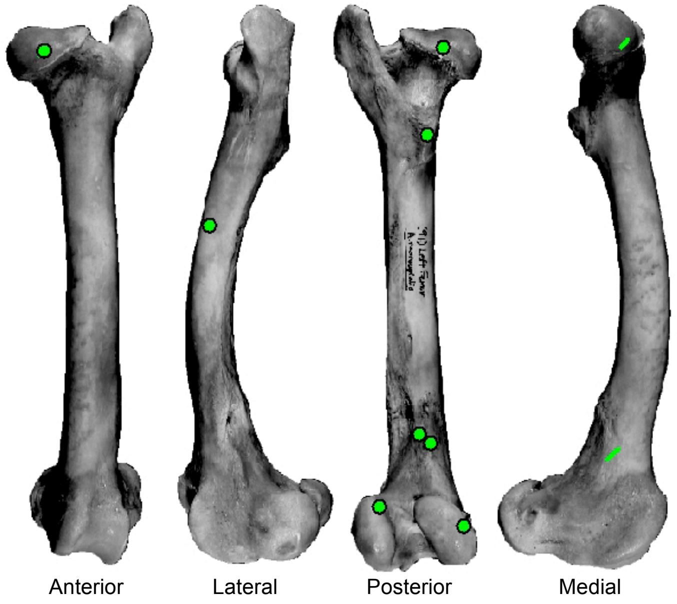
APPENDIX B

FIGURES DISPLAYING DISTRIBUTION OF BONE MODIFICATIONS BY ELEMENT IN THE KANJERA SOUTH ASSEMBLAGE AND IN EXPERIMENTAL ASSEMBLAGES REFERRED TO IN TEXT

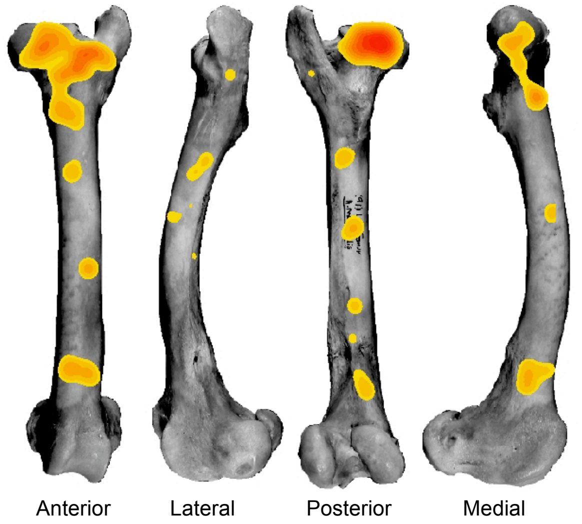
Images represent right/left composites (on left side templates) of hominin- and carnivore-induced modifications in beds KS-1–KS-3. Modification patterns are similar across beds, so combined data for all beds are presented in these images. Small/medium sized bovids (size 1-3a) at Kanjera are combined as sample sizes are not large enough to display modifications separately by size class. Large carcasses (size 3b) are shown separately, although not all elements bear marks.

Figure B.1. Distribution of carnivore damage on the femora at Kanjera South and in experimental assemblages (small and medium bovids combined). Where sample sizes are large enough, GIS density analyses are shown. Where sample sizes are small, distribution of individual tooth marks is shown. N = the number of specimens bearing tooth marks. The canid experimental model is compared with Kanjera small/medium bovids as the sample size is small for Blumenschine's carnivore only hyaenid experiments.

Kanjera Carnivore Damage to Small and Medium Bovids
n = 6



Carnivore Only tooth mark distribution (Canid)
n = 110



Hammerstone → Carnivore tooth mark distribution n = 4

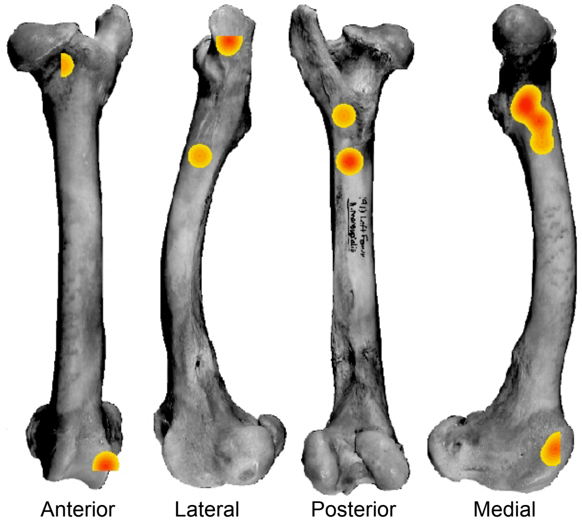
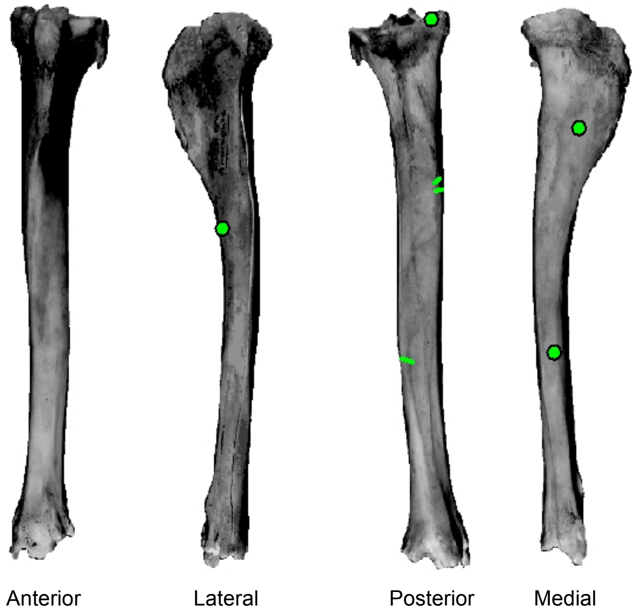
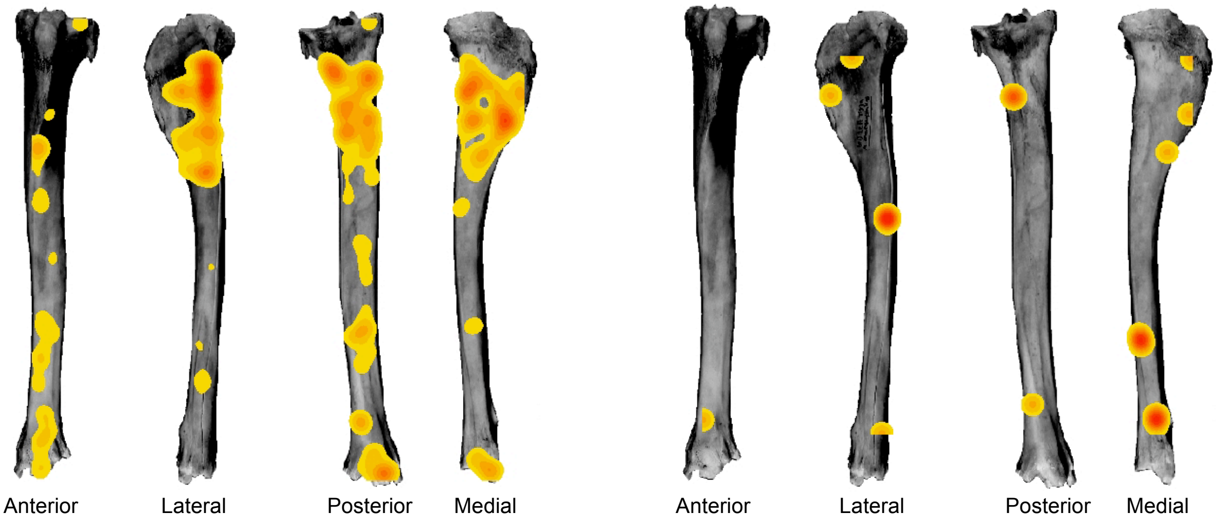


Figure B.2. Distribution of carnivore damage on the tibiae at Kanjera South and in experimental assemblages (small and medium bovids combined). See fig. B.1 caption for details.



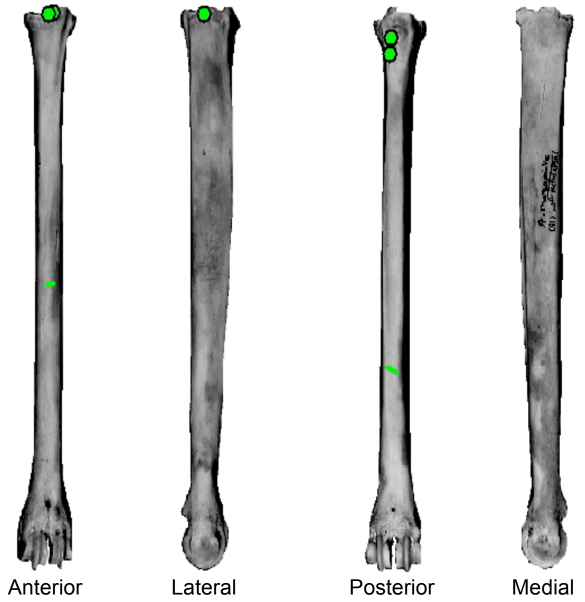
Kanjera Carnivore Damage to Small and Medium Bovids
n = 5



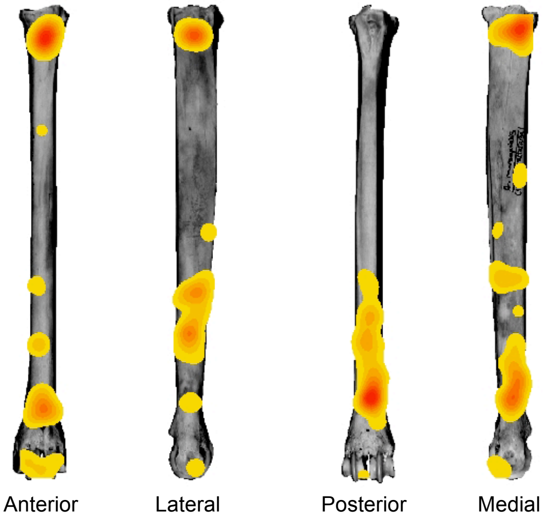
Carnivore Only tooth mark distribution (Canid)
n = 134

Hammerstone → Carnivore tooth mark distribution n = 6

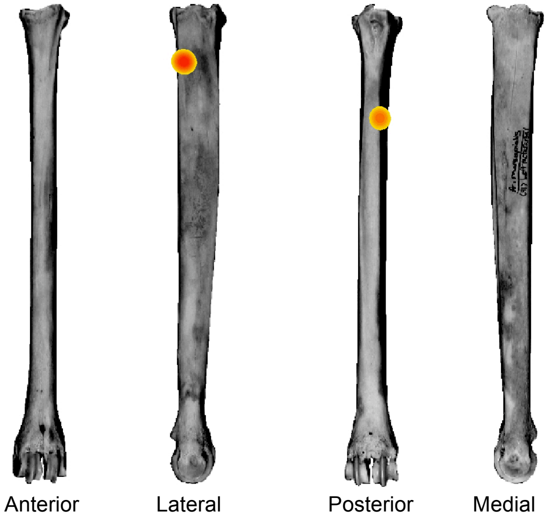
Figure B.3. Distribution of carnivore damage on the metatarsals at Kanjera South and in experimental assemblages (small and medium bovids combined). See fig. B.1 caption for details.



Kanjera Carnivore Damage to Small and Medium Bovids
n = 5

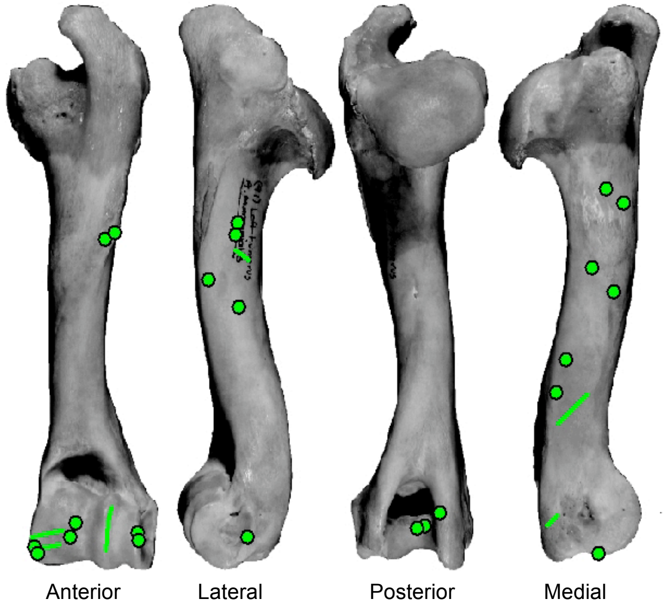


Carnivore Only tooth mark distribution (Canid)
n = 73

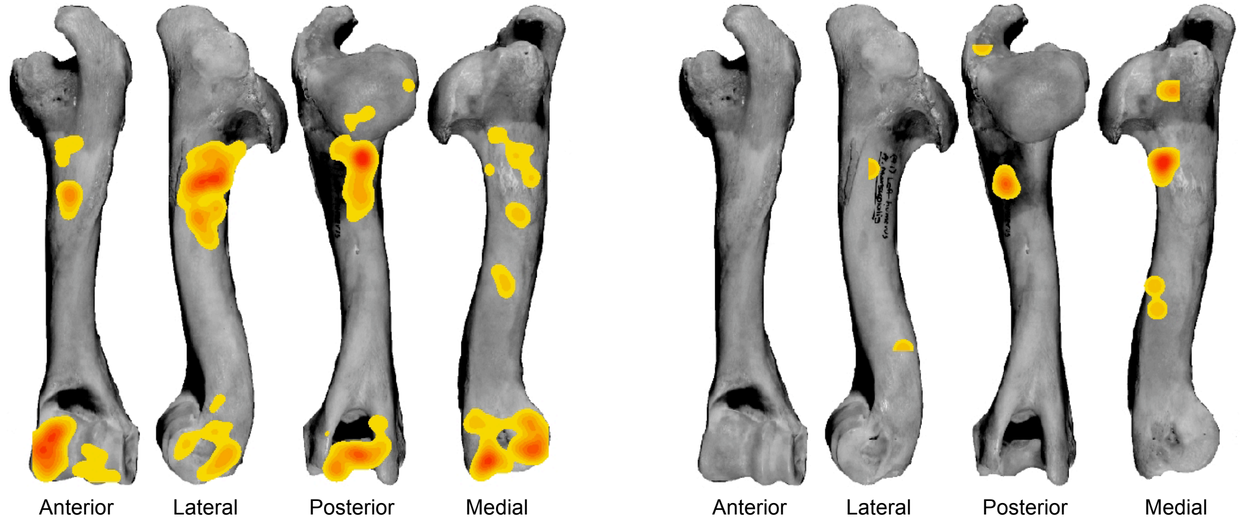


Hammerstone → Carnivore tooth mark distribution n = 1

Figure B.4. Distribution of carnivore damage on the humeri at Kanjera South and in experimental assemblages (small and medium bovids combined). See fig. B.1 caption for details.



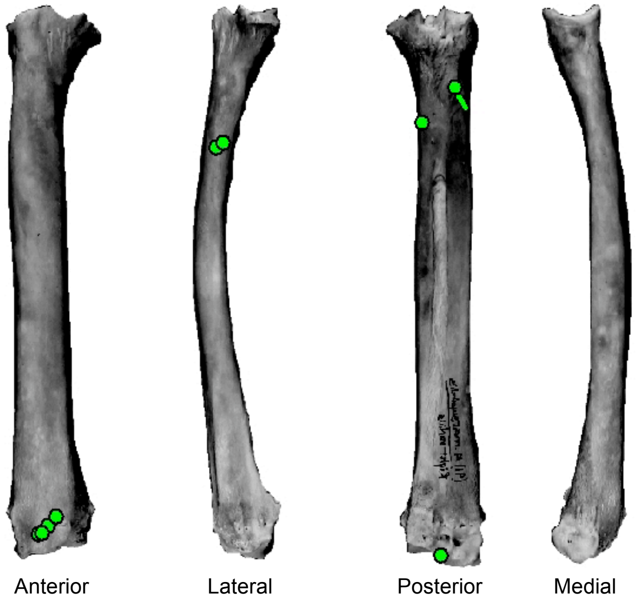
Kanjera Carnivore Damage to Small and Medium Bovids
n = 11



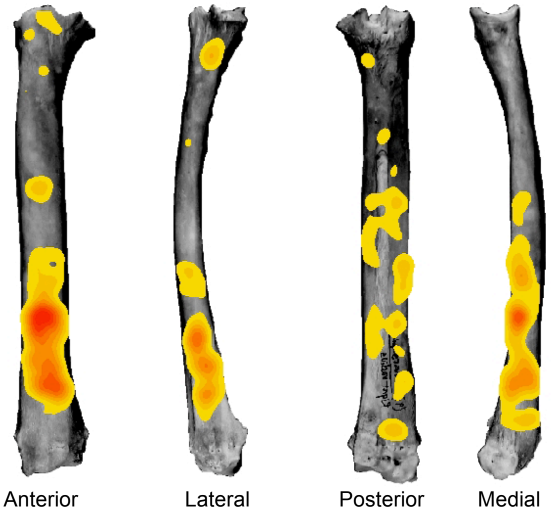
Carnivore Only tooth mark distribution (Canid)
n = 119

Hammerstone → Carnivore tooth mark distribution n = 5

Figure B.5. Distribution of carnivore damage on the radii at Kanjera South and in experimental assemblages (small and medium bovids combined). See fig. B.1 caption for details.



Kanjera Carnivore Damage to Small and Medium Bovids
n = 5

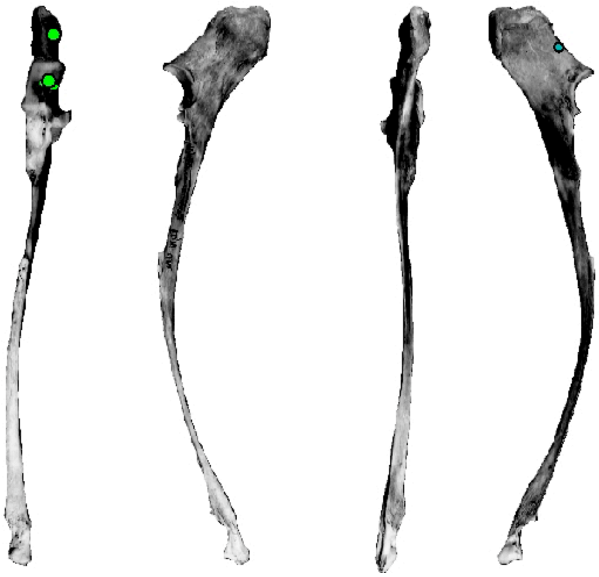


Carnivore Only tooth mark distribution (Canid)
n = 113

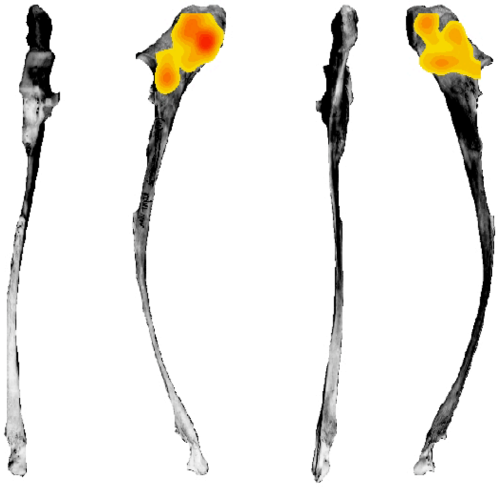
Hammerstone → Carnivore tooth mark distribution N/A

Figure B.6. Distribution of carnivore damage on the ulnae at Kanjera South and in experimental assemblages (small and medium bovids combined). See fig. B.1 caption for details.

Kanjera Carnivore Damage to Small and Medium Bovids
n = 1



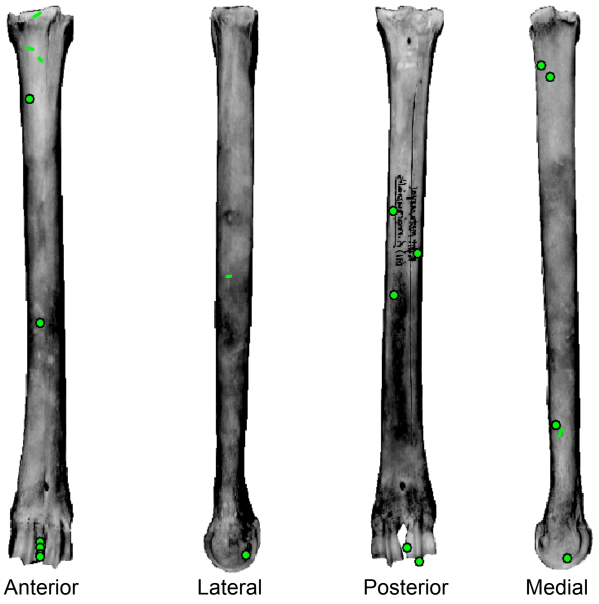
Carnivore Only tooth mark distribution (Canid)
n = 59



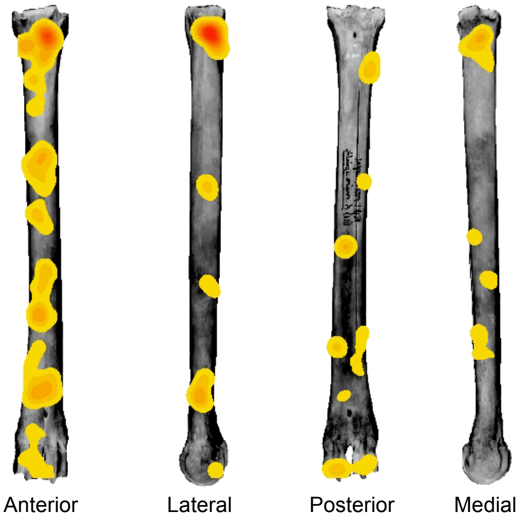
Hammerstone → Carnivore tooth mark distribution N/A

Figure B.7. Distribution of carnivore damage on the metacarpals at Kanjera South and in experimental assemblages (small and medium bovids combined). See fig. B.1 caption for details.

Kanjera Carnivore Damage to Small and Medium Bovids
n = 7



Carnivore Only tooth mark distribution (Canid)
n = 73



Hammerstone → Carnivore tooth mark distribution n = 1

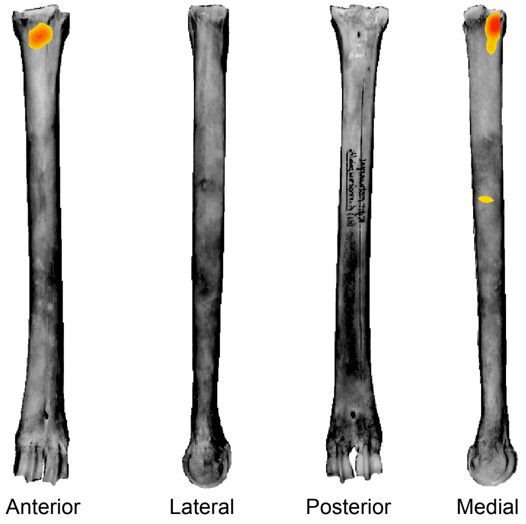


Figure B.8. Distribution of carnivore damage on large bovid forelimbs in experimental assemblages. a. humerus, b. radio-ulna, B. metacarpal, n/a experiments not available.

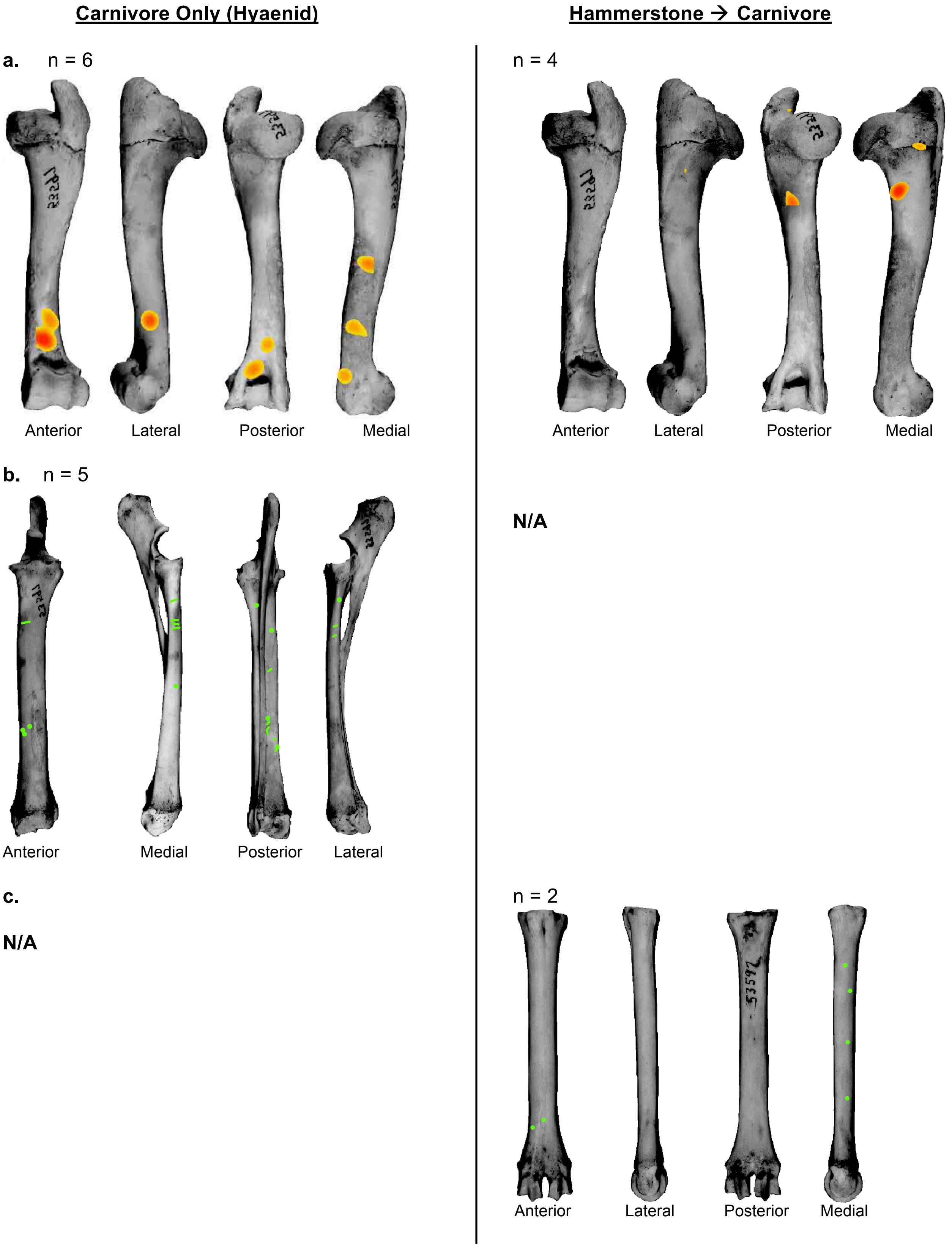


Figure B.9. Distribution of carnivore tooth marking on large bovid hindlimbs in experimental assemblages. a. femur, b. tibia, c, metatarsal, , n/a experiments not available

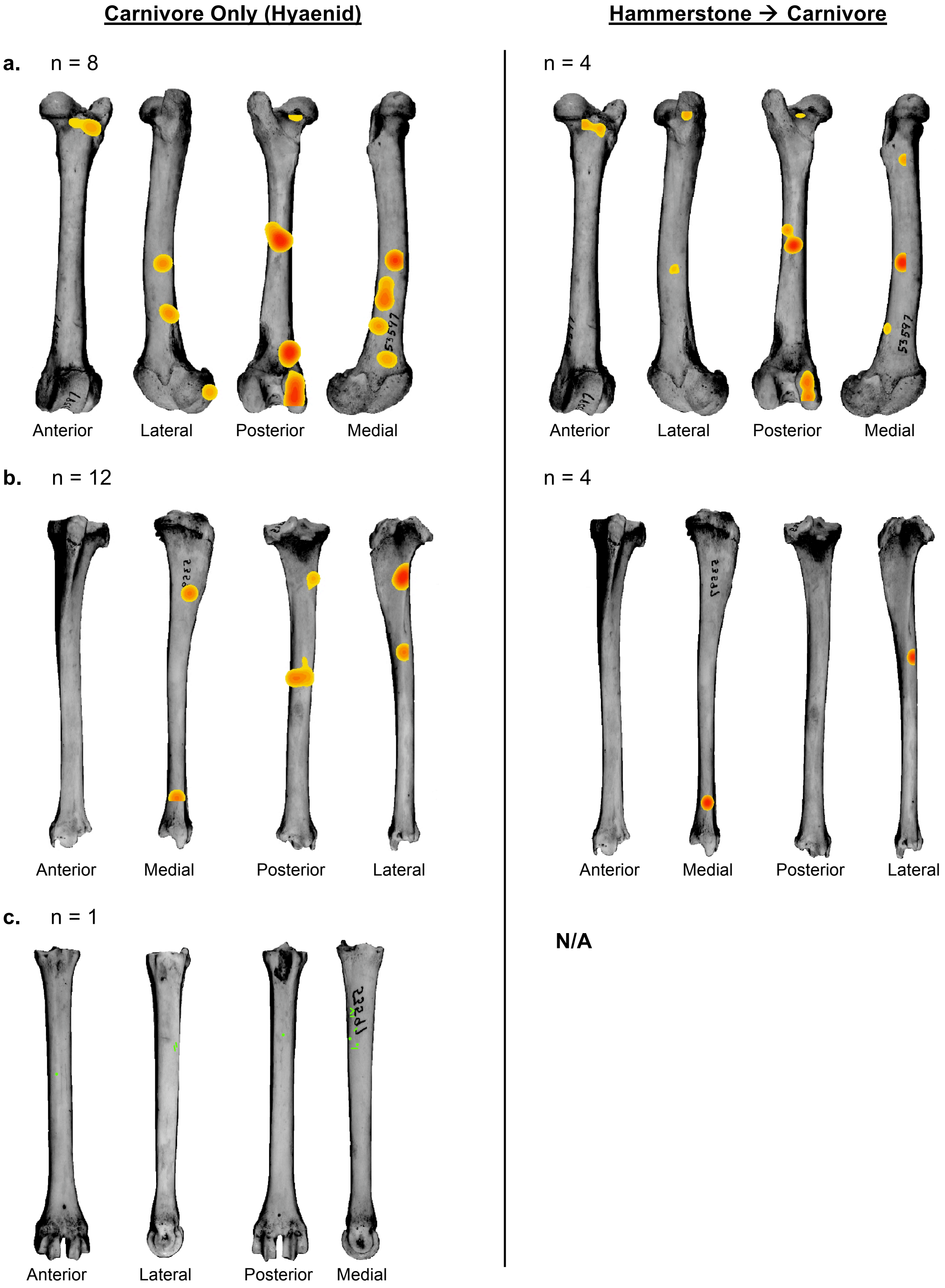
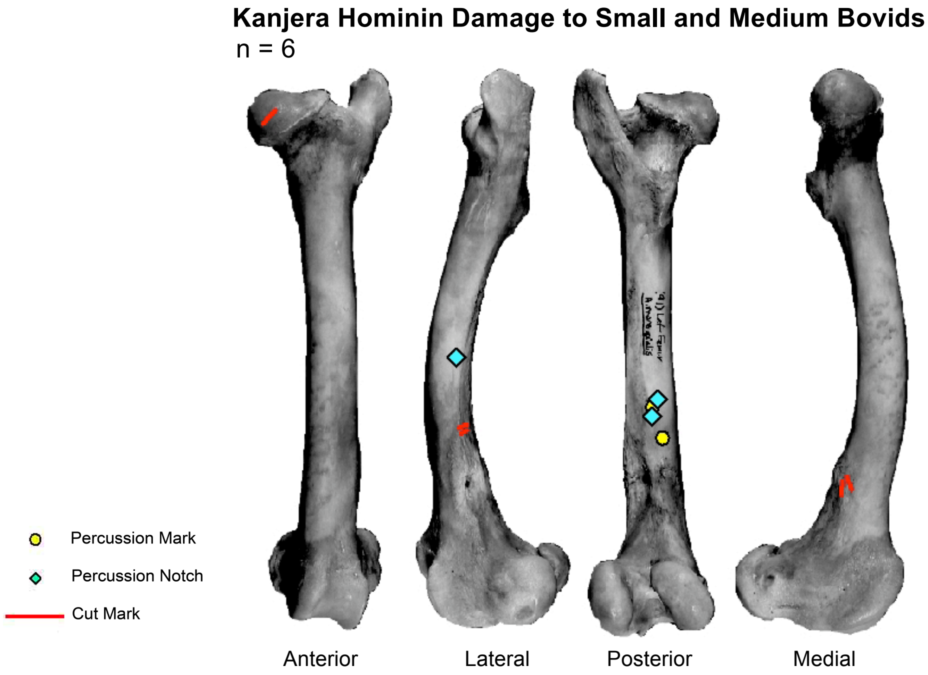
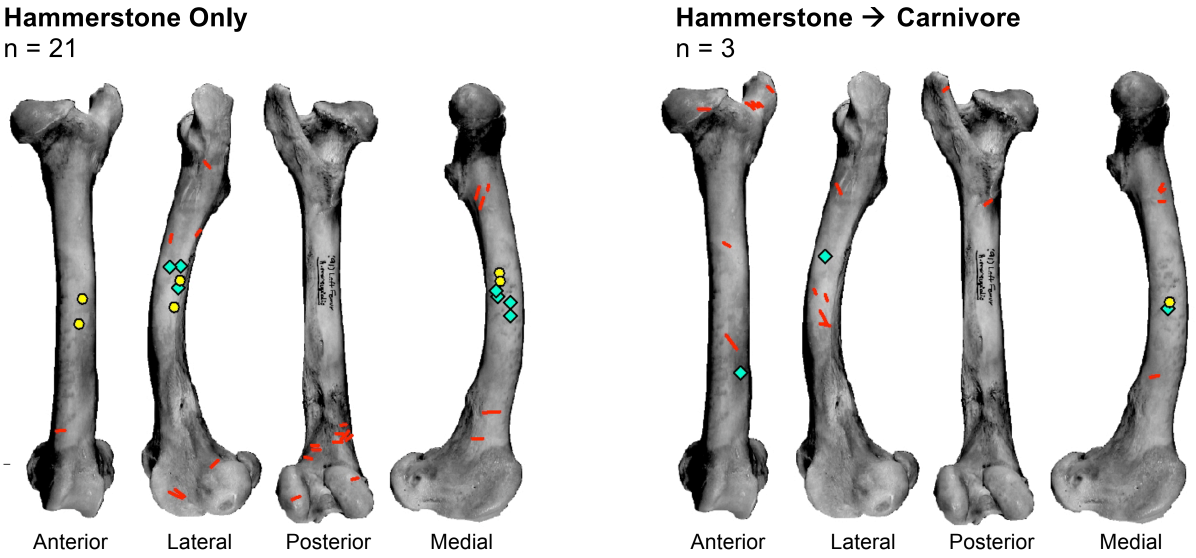


Figure B.10. Distribution of cut and percussion marking on the femora at Kanjera South and in experimental assemblages (small and medium bovids combined). Small bovids = size class 1, medium bovids = size class 2-3a. Hominin-induced damage includes cut marks, percussion notches, and percussion marks.


Kanjera Hominin Damage to Small and Medium Bovids
n = 6


Hammerstone Only
n = 21

Hammerstone → Carnivore
n = 3

Figure B.11. Distribution of cut and percussion marking on the tibiae at Kanjera South and in experimental assemblages (small and medium bovids combined). See Fig. B.10 for details.

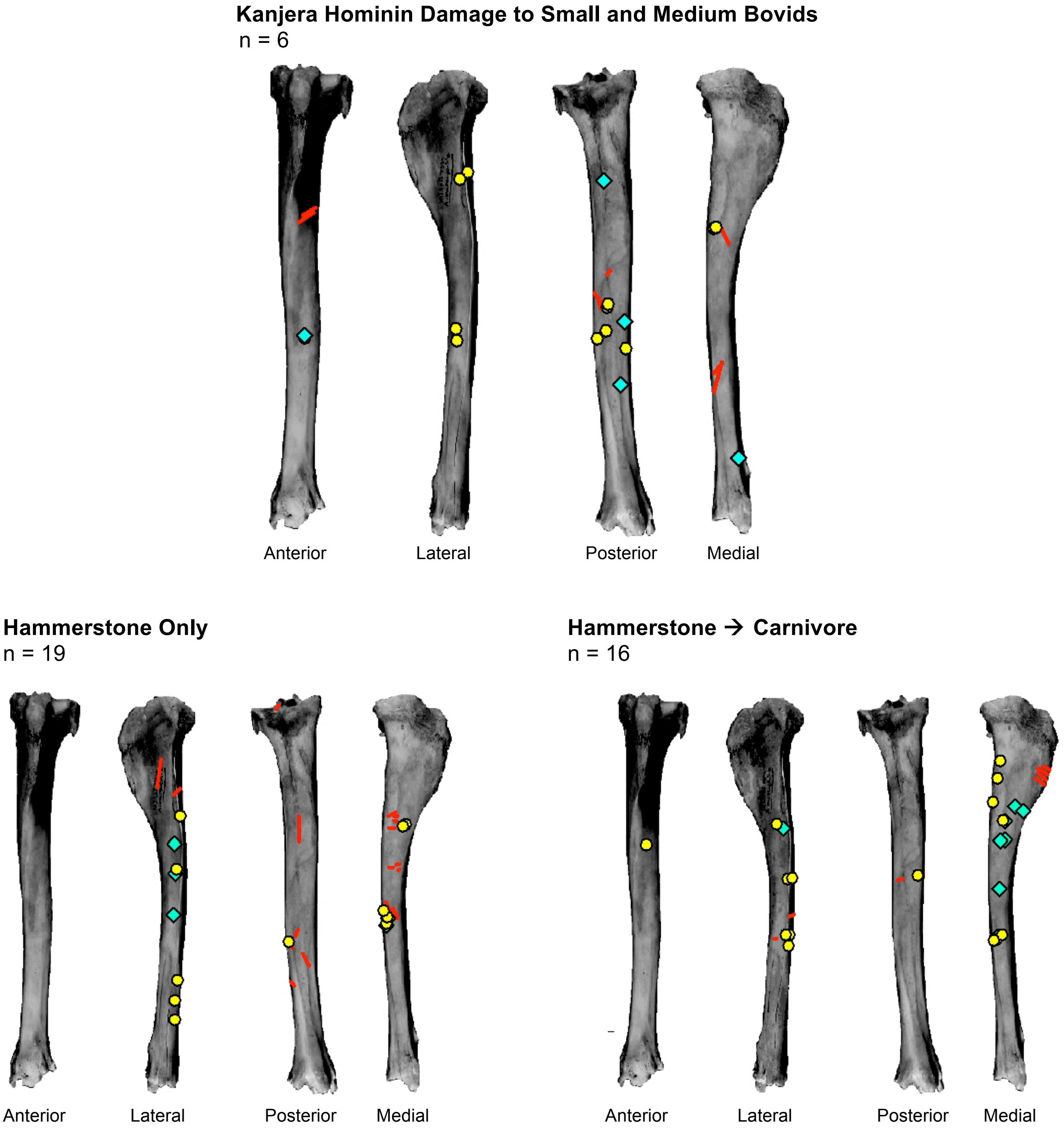
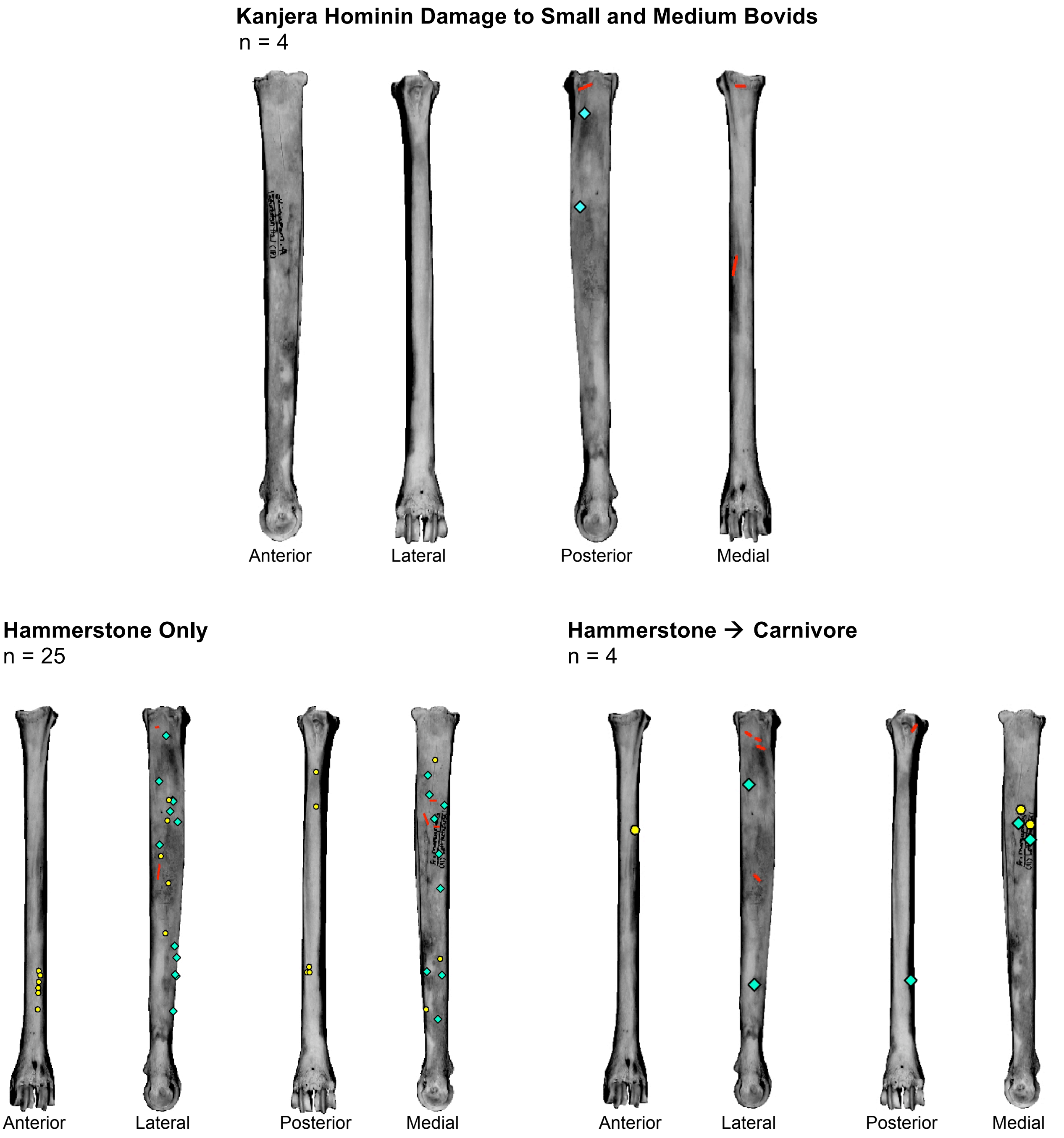


Figure B.12. Distribution of cut and percussion marking on the metatarsals at Kanjera South and in experimental assemblages (small and medium bovids combined). See Fig. B.10 for details.

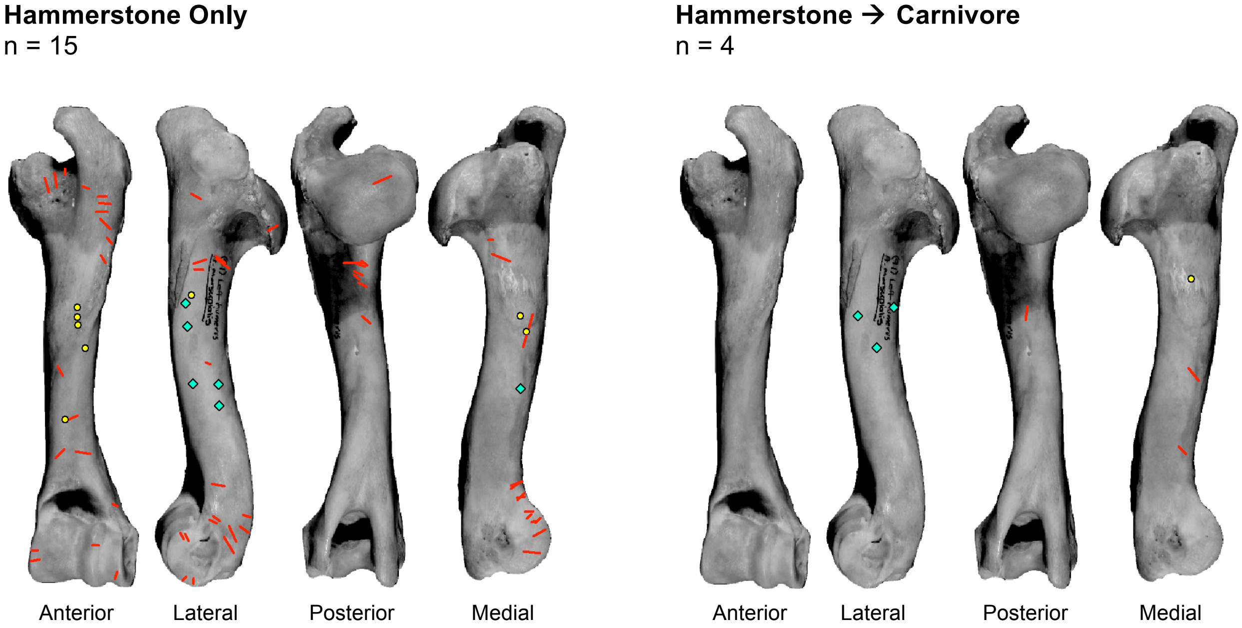


Kanjera Hominin Damage to Small and Medium Bovids
n = 4

Hammerstone Only
n = 25

Hammerstone → Carnivore
n = 4

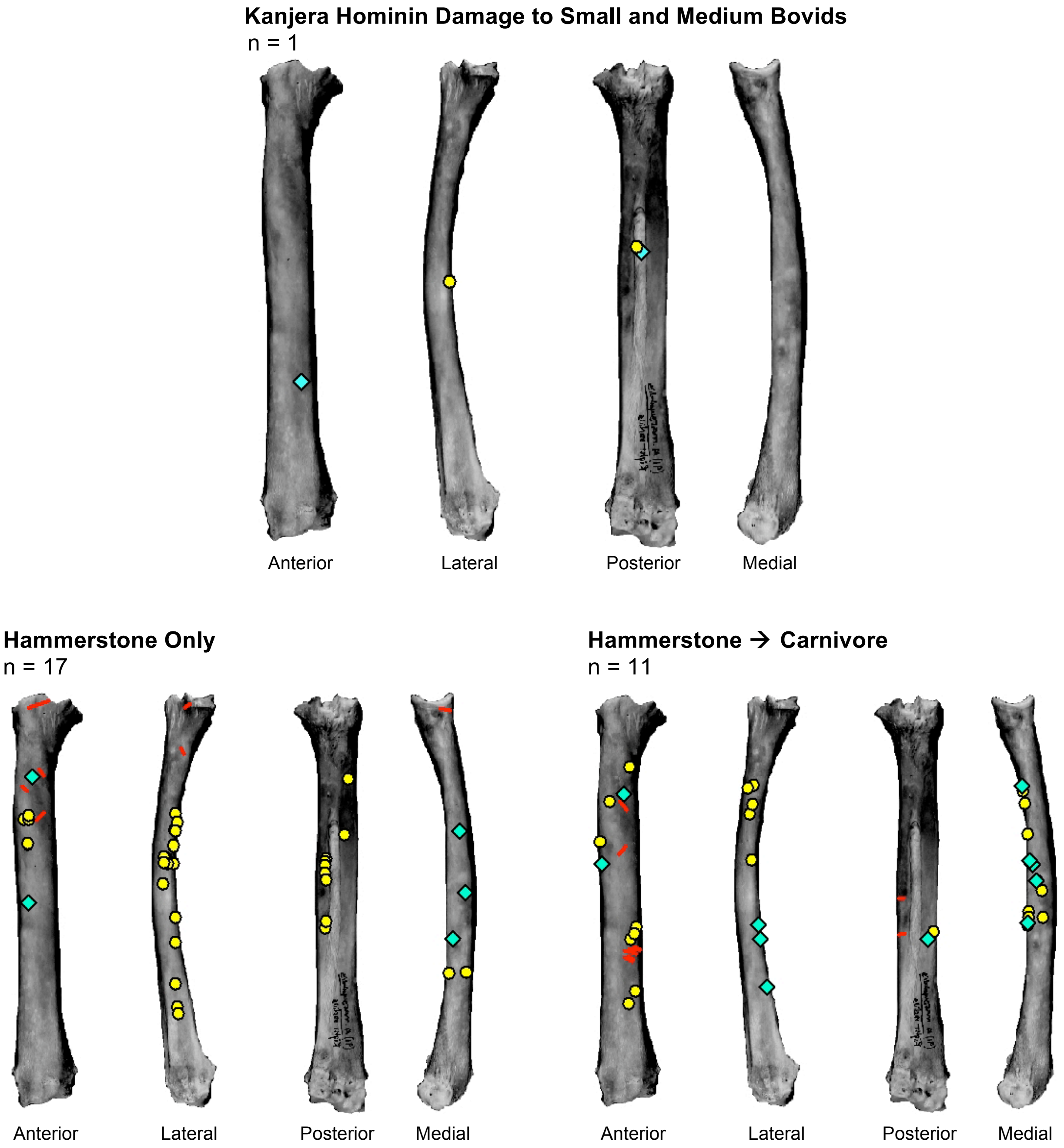
Figure B.13. Distribution of cut and percussion marking on the humeri in experimental assemblages (small and medium bovids combined). No small or medium sized bovid humeri from KJS display hominin modifications. See Fig. B.10 for details.



Hammerstone Only
n = 15

Hammerstone → Carnivore
n = 4

Figure B.14. Distribution of cut and percussion marking on the radii at Kanjera South and in experimental assemblages (small and medium bovids combined). See Fig. B.10 for details.

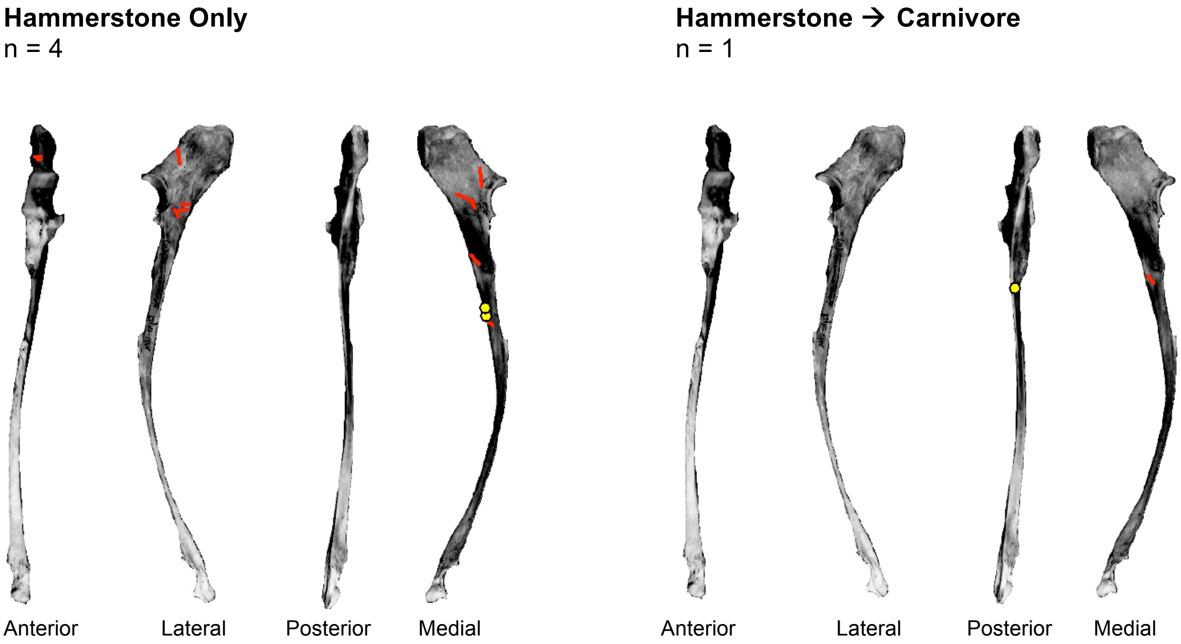


Kanjera Hominin Damage to Small and Medium Bovids
n = 1

Hammerstone Only
n = 17

Hammerstone → Carnivore
n = 11

Figure B.15. Distribution of cut and percussion marking on the ulnae in experimental assemblages (small and medium bovids combined). No small or medium sized bovid ulnae from KJS display hominin modifications. See Fig. B.10 for details.

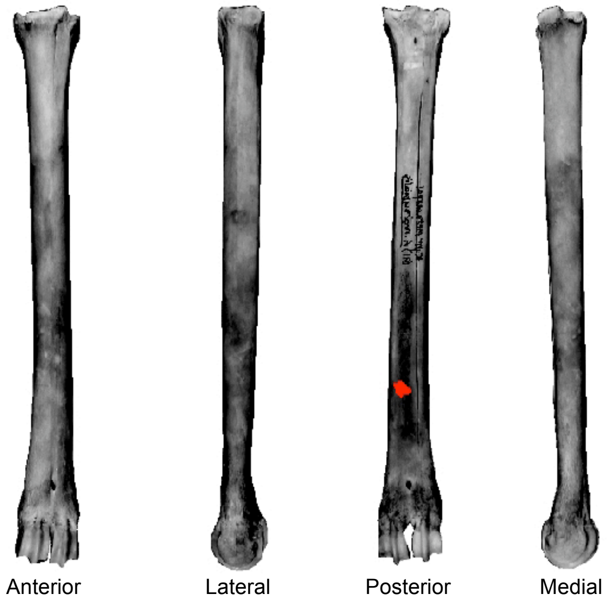


Hammerstone Only
n = 4

Hammerstone → Carnivore
n = 1

Figure B.16. Distribution of cut and percussion marking on the metacarpals at Kanjera South and in experimental assemblages (small and medium bovids combined). See Fig. B.10 for details.

Kanjera Hominin Damage to Small and Medium Bovids
n = 1



Hammerstone Only
n = 25

Hammerstone → Carnivore
n = 3

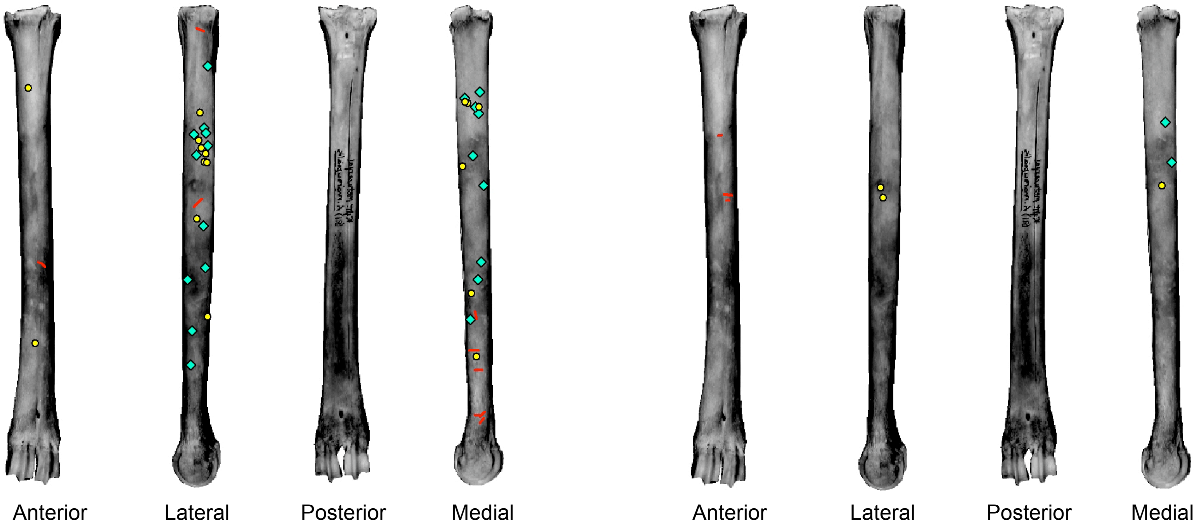
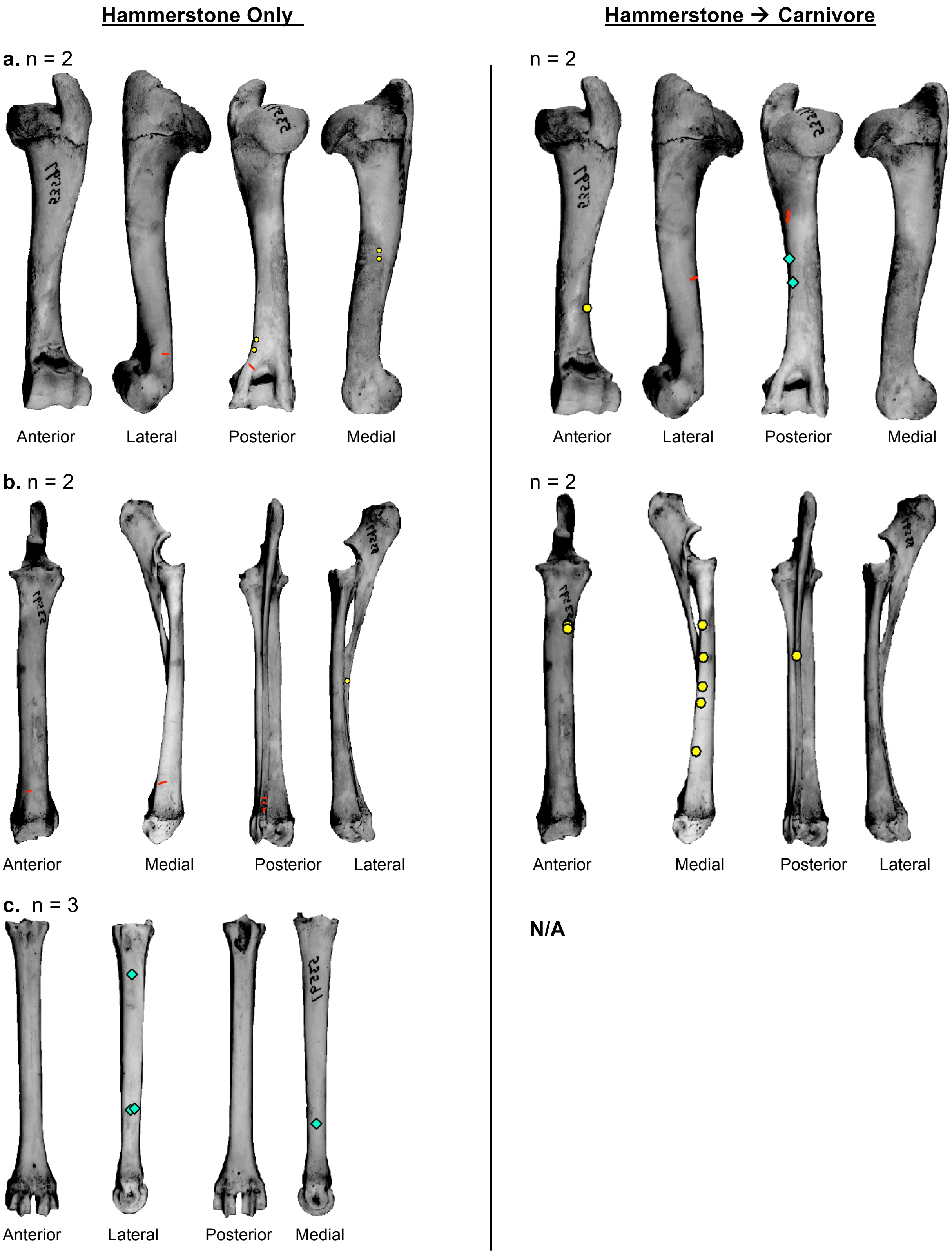


Figure B.17. Distribution of human-induced damage on large bovid (size 3b) limbs in experimental assemblages. a. humerus, b. radio-ulna, c, metatarsal (other elements not preserved).



APPENDIX C

LIST SPECIMENS FROM KANJERA SOUTH BEARING CARNIVORE AND HOMININ MODIFICATIONS

Table C.1. List of tooth marked specimens from Kanjera used in GIS study
Previous ID shows how this modification was identified by 3 other observers in Ferraro's (2007) study. If Previous ID field is blank, data are not available. This is the case for new specimens from the 2009 excavation that have not been previously studied. P = tooth pit, S = tooth score, B = both tooth pit and score.

Field #	Carnivore surface damage type	Previous ID	Element
Bed 1			
4072	B	p/b/b	MC
4195	P	n/p/p	MT
4197	B	b/b/b	MC
4512a	B	p/p/b	Hum
4540	P	p/n/n	Rad
4541	P	p/n/n	Hum
4610	P	n/p/n	Rad
4627	S	s/n/n	Fem
4644	B	-	Uln
4874	P	b/b/b	Hum
4898	P	n/p/p	Tib
5385	P	-	MC
6105	S	s/s/s	Fem
6105 (duplicate)	P	-	Fem
6236	B	b/b/b	MT
21387a	P	n/p/n	Fem
24003	P	-	Hum
Bed 2			
96	B	b/b/b	Fem
112	P	p/p/p	Hum
325	S	-	Hum
771	P	p/p/p	Rad
2565	P	n/p/n	Fem
4271a	P	-	Hum
4781	P	-	Rad
5527	P	p/n/n	MC
6102	P	-	Tib
7472	S	n/s/s	MT
(9633)	P	p/p/p	Hum

9685	S	s/s/n	Hum
9734a	P	p/p/p	Hum
11610	S	s/s/s	MT
12573	B	p/b/b	Fem
13336	P	b/b/b	Rad
13885	B	s/s/s	MC
13891	P	n/p/n	Tib
13898	P	-	MT
17740	S	s/b/n	Rad
18347	P	n/p/p	MT
21006	S	s/s/s	Tib
23525	P	p/n/n	MC
24659	P	p/p/n	Hum
Bed 3			
24	P	p/p/n	MC
322	P	-	Tib

Table C.2. List of cut marked specimens from Kanjera used in GIS study
Specimens in this list were identified by me as bearing at least one cut mark. Previous ID shows how many of the observers from Ferraro's (2007) study also identified the specimen as being cut marked. If Previous ID field is blank, data are not available. This is the case for new specimens from the 2009 excavation that have not been previously studied.

Field #	**Previous ID**	**Element**
Bed 1		
5387a	2/3	Tib
6014	3/3	MC
6105	-	Fem
Bed 2		
2565	3/3	Fem
3321	2/3	MT
5317	2/3	Tib
7472	2/3	MT
9805	2/3	Rad
13336	2/3	Rad
24183	-	Fem
24759	-	MT
Bed 3		
322	3/3	Tib
(7111)	-	Tib
7379	3/3	Hum

Specimens in parentheses are from Conglomerate patches.

Table C.3. List of specimens from Kanjera bearing percussion marks and notches used in GIS study
Specimens in this list were identified by me as bearing at percussion damage. Previous ID shows how many of the observers from Ferraro's (2007) study also identified percussion damage on the specimen. If Previous ID field is blank, data are not available. This is the case for new specimens from the 2009 excavation that have not been previously studied. PM = percussion mark (pit or striae), PN = percussion notch.

Field #	**Percussion Mark**	**Previous ID**	**Percussion Notch**	**Previous ID**	**Element**
Bed 1					
3511	PM	0/0	PN	2/3	Rad
5268			PN	3/3	Fem
5387a	PM	3/3			Tib
22222	PM	3/3	PN	2/3	Fem
25126	PM	-	PN	-	Tib
Bed 2					
1159			PN	-	Tib
2893			PN	3/3	Hum
5317	PM	3/3	PN	0/0	Tib
5951	PM	3/3	PN	0/0	Hum
6378			PN	3/3	MT
9805	PM	3/3			Rad
Bed 3					
64	PM	3/3	PN	3/3	Fem
323	PM	1/3	PN	0/0	Tib
7379	PM	0/0*	PN	3/3	Hum
(7111)	PM	-			Tib

*This was classified by all three other observers as a cut mark

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