Early Hominid Hunting and Scavenging: A Zooarchaeological Review

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Before the early 1980s, the prevailing orthodoxy in paleoanthropology considered Early Stone Age archeological sites in East Africa to represent a primitive form of hominin campsites. The faunal evidence preserved in these sites was viewed as the refuse of carcass meals provided by hominid males in a social system presumptively characterized by sexual division of labor. This interpretation of early hominin life ways, commonly known as the “Home Base” or “Food Sharing” model, was developed most fully by Glynn Isaac. As Bunn and Stanford emphasized, this model was greatly influenced by a paradigm that coalesced between 1966 and 1968, referred to as “Man the Hunter.”

Opposition to what was perceived as gender bias in the “Home Base-Food Sharing” model followed soon after Isaac’s early statement of that model. However, most of this initial criticism did not deal specifically with the Plio-Pleistocene archeological record, but rather was a scientifically couched commentary on a preoccupation by some male researchers with the assumed predatory nature of male early hominids. It was not until 1981 that an archeologically based challenge was leveled at the “Home Base-Food Sharing” model. Lewis Binford’s interpretation of the archeofauna from FLK 22 Zinjanthropus (FLK Zinj), a 1.75 million-year-old (Ma) purported hominid home base site at Olduvai Gorge, Tanzania, was the basis of the “Obligate Marginal Scavenger” model. This model stated that hominids, as passive scavengers of carnivore-killed carcasses, played only a minor role in site formation at FLK Zinj.

In the time since Binford’s “Obligate Marginal Scavenger” model, other researchers have argued that Plio-Pleistocene hominids selected specific, desirable areas on the landscape to which they transported gathered food, including large mammal carcass resources, and at which they carried out activities such as stone tool manufacturing. This model, best expressed as the “Central Place Foraging” model, is really only a slight reworking of Isaac’s original “Home Base-Food Sharing” model and was, indeed, propounded by Isaac in the wake of Binford’s critique. (We do note that the “Central Place Foraging” model was not necessarily a reaction to the “Obligate Marginal Scavenger” model, even though Isaa’c’s “Central Place Foraging” model was formally published in 1983, two years after Binford’s book Bones: Ancient Men and Modern Myths. As early as 1981, discussed the idea that archeological sites may have formed from the simple repeated use of the same attractive locales by hominids rather than as the result of activities predicated on the type of “social contract” implied by the “Home Base-Food Sharing” model. (This idea has been further developed subsequently by other researchers.)

Endowing hominids with a somewhat different type of intentionality, the “Stone Cache” model advanced the notion that early hominids used specific locales—at which they had previously stored stone-tool raw materials—as carcass-processing sites in order to avoid competing with carnivores for those carcasses elsewhere on the ancient landscape. This idea was reworked in the “Refuge” model. Proponents of this model see archeological sites as loci at which the accumulation of large mammal bones was the result of hominids’ long-term, unintentional reuse of the same places as carnivore-avoidance refuges.

Variation on the “Refuge” model theme can be recognized in other ideas of archeological site formation in the Early Stone Age, with some researchers positing that early hominids simply revisited the same spots on the landscape habitually, in much the same way that modern chimpanzee repeatedly use the same nesting sites. Just as modern chimpanzee nest sites are recognizable by dung, hair, and modification of trees, so are
the “favored places” (also referred to as “referential places” or “focal places”29–31) of early hominids archeologically recognizable by such material consequences of their subsistence activities as stone tools and butchered animal bones.

A dissenting opinion on the formation of Early Stone Age archeofaunas has been proffered by O’Connell,32 who suggests that these accumulations may represent “near-kill” locations rather than transported assemblages.32 Such near-kill locations would be similar to those created by a group of modern foragers, the Hadza (Tanzania), where they prepare large mammal carcasses for transport elsewhere.

In review, we believe that each of the models constructed since Isaac’s articulation of the “Home Base-Food Sharing” model can be accommodated in one of two major groups. The first group of models posits the acquisition of whole or substantial portions of large mammal carcasses by hominids and subsequent transport of these resources to favored locales for processing, consumption, and possibly for sharing. This group of models implies that hominids gained access to large mammal carcasses before or very shortly after carnivore involvement. This, in turn, indicates hominid proficiency in hunting and/or confrontational scavenging. The second group of models posits infrequent acquisition of substantial carcass resources by hominids, insufficient for any kind of regular meat sharing. This group of models relegates hominids to the role of passive scavengers who obtained carcass resources only after they had been abandoned by dominant carnivore competitors. Here we review and evaluate the zooarcheological and actualistic data used to support these divergent views of early hominid foraging capabilities—a component of behavioral ecology that is essential to a more complete understanding of our Plio-Pleistocene ancestors.

SKELETAL PART PROFILES: EARLY APPLICATIONS AND SUBSEQUENT DIFFICULTIES

Initially, analysis of the abundance of skeletal elements was the foundation for models of large-mammal carcass acquisition and use by early hominids. Based on the assumption that there are taxonomically diagnostic patterns in the way in which modern humans, their hominid ancestors, and other biotic actors such as carnivores transport and accumulate large-mammal carcass parts, skeletal part profiles were used to discern the agents of bone collection in archeological sites. This assumption largely arises from the early work of White33 and Perkins and Daly,34 who claimed that humans typically reduce large mammal carcasses at acquisition sites and then transport certain carcass units more regularly than others to sites of accumulation (the so-called schlepp effect). Interestingly, White and Perkins and Daly disagreed on exactly which carcass parts humans usually transported: White purported the preferential transport of limb units, while Perkins and Daly argued for preferential transport of axial units and foot bones. Thus, much subsequent ethnarcheological work has been devoted to recording carcass-part transport by extant foraging groups.35–43 While there is still much debate about whether there is, in fact, a consistent “human pattern” of bone transport, most zooarcheological applications of these actualistic data view high representation of limb bones as indicating a transported assemblage and, conversely, a high representation of axial bones as representing a kill or acquisition site.12,18–21

It is important to note, however, that limb-dominated assemblages also characterize some carnivore-created accumulations.12 This complicates matters for zooarcheologists reliant on skeletal-part ratios to construct interpretative scenarios because faunas recovered in most East African Plio-Pleistocene sites are, in fact, dominated by limb bones and head elements.18,21,44 Thus, based solely on skeletal element representation, these fossil faunas could be viewed as the product of early access by hominids to carcasses with fully fleshed limbs16–21,45 or the residues of carnivore kills picked over by hominids.12,46 A similar pattern of skeletal part representation has even been observed in modern, experimentally created sites, in which small ungulate carcasses were ravaged by spotted hyenas after those carcasses had been butchered by human researchers.47 Actualistic work conducted by Blumenschine and his colleagues in the mid-1980s through the mid-1990s seems, in part, a response to these ambiguities arising from a reliance on skeletal-part profiles. Based on this work, Blumenschine46–53 argued that hominids were primarily passive scavengers who concentrated not on meat scraps, but rather on the marrow remaining in ungulate limb bones after they had been defleshed and abandoned by primary carnivore consumers. While these conclusions are not accepted by all paleoanthropologists, one of the most important contributions of this body of work was a reemphasis on the important role carnivores played in the formation of most Early Stone Age archeological sites regardless of the relative contribution of hominids to the material remains recovered from those sites. This perspective was the result of an analytical focus on bone-surface damage in experimentally derived and actual archeological assemblages, in addition to the study of skeletal-part ratios. Although Blumenschine and his colleagues were not the first researchers...
to understand the importance of the co-occurrence of hominid-inflicted tool marks (cutmarks and hammerstone percussion damage) and carnivore tooth marks in the same archaeofauna.\textsuperscript{12,16–21,26,54} they did introduce important new methods of quantifying different classes of bone damage per specific bone portion in order to ascertain the relative timing of hominid versus carnivore influences on those assemblages.

While Blumenschine and his colleagues constructed actually derived models of multiple-pattern faunal assemblages,\textsuperscript{50–53,55–60} other research demonstrated additional weaknesses of the utility of skeletal-part ratios for inferring the bone-collecting behavior of prehistoric agents. This research emphasized the important role of bone mineral density in the differential survival of skeletal parts when a bone assemblage is subjected to destructive forces, regardless of the agents applying those forces.\textsuperscript{51–78}

**BONE SURFACE MODIFICATIONS AND THE UTILITY OF MULTIPLE-PATTERN MODELS**

The multiple-pattern models of archaeofauna formation developed by Blumenschine and his colleagues have impressive explanatory power on several levels, the most basic of which is that they confront the fact that most Early Stone Age faunal assemblages display incidences of both hominid-inflicted tool marks and carnivore-inflicted tooth marks.\textsuperscript{18,24,44,54} However, we believe that there is a crucial weakness in these widely influential models. That weakness is a focus on the importance of the evidence of hammerstone percussion damage and carnivore tooth marks, combined with less serious consideration of the abundant cutmark evidence also preserved in most Plio-Pleistocene archaeofaunas. We believe further that this analytical imbalance compromises the reconstructions of early hominid carcass-foraging behavior emanating from these models.

The models developed by Blumenschine and his colleagues are sophisticated, but their basic assumptions are straightforward and commonsensical. Carnivore tooth marks on bones result from the consumption of meat overlying those bones and from the extraction of marrow and grease contained within them. Thus, the presence and quantity of carnivore tooth marks on a bone or bone portion are linked directly with the amount of these associated, edible resources that was available to a carnivore at the time it acquired the carcass.\textsuperscript{55} Based on experiments with naturally occurring ungulate carcasses and simulated archeofaunal sites (that is, sites created by the researcher, containing humanly defleshed and/or demarrowed ungulate bones), Blumenschine observed that the percentage of carnivore tooth marks on sections of ungulate limb bones varies according to the timing of carnivore access to a carcass.\textsuperscript{50} As a function of defleshing activities (in the case of large felids) and defleshing and/or demarrowing activities (in the cases of hyenids and canids), a carnivore that has primary access to a fully fleshed carcass imparts tooth marks on a high percentage of midshaft sections of limb bones. Most often in such cases, more than 75% of all recovered limb bone midshaft sections bear tooth marks. This is because midshaft sections of upper (humerus and femur) and intermediate (radio-ulna and tibia) limb bones are heavily muscled and also encase substantial marrow reserves, the edible resources sought by consumers. On the other hand, when carnivores are confronted with previously defleshed and demarrowed bones in the simulated archeofaunal sites, many fewer limb bone midshaft sections have tooth marks (5% to 15% of recovered specimens) because these bone sections are no longer associated with edible resources when carnivores finally gain access to them.\textsuperscript{50,57}

The FLK Zinj archeofauna, because of its finely preserved bone surfaces, was a prime assemblage in which to apply this referential framework.\textsuperscript{52} Blumenschine,\textsuperscript{52} Selvaggio,\textsuperscript{55,56} and Capaldo\textsuperscript{57–60} all concluded that this large fossil assemblage (containing more than 3,500 identifiable bone specimens,\textsuperscript{18,21}) resulted from the activities of three separate genera of prehistoric consumers. First large felids presumably killed or otherwise gained early control of ungulate carcasses, and thoroughly defleshed most or all of the limb bones. After feld abandonment of these carcasses, hominids scavenged the defleshed but marrow-filled limb bones, taking them to the locale of FLK Zinj. There the hominids hammered open the bones to harvest the marrow. Finally, hyenas, equipped with the anatomical apparatuses and physiological capabilities to extract nutrients from cancellous bone, scavenged the grease-laden epiphyses ignored by hominids, who were morphologically and technologically unequipped to render this valuable bone food resource.

According to Blumenschine, Selvaggio, and Capaldo, this multiple-pattern sequence of carcass use and assemblage formation is supported by the percentages and distributions of tooth marks and hammerstone percussion marks across various sections of limb bones in the fossil assemblage. The frequency of tooth marks on limb bone midshaft portions in the FLK Zinj archeofauna is high, close to the percentage observed in experiments in which carnivores had primary access to ungulate limbs.\textsuperscript{50,52,55–58} In addition, the high frequency of hammerstone percussion marks in the archeological assemblage suggests that these initial carnivore consumers did not break open the limb bones for marrow, leaving this resource available to hominids using stone hammers. Finally, abundant tooth marks on limb-bone epiphyses and metaphyses suggest that these grease-bearing portions were ignored by hominids but subsequently exploited by hyenas.

Discussion of the abundant cutmark evidence preserved in the FLK Zinj archeofauna\textsuperscript{17–21,54,79} is not emphasized in this model because of a perception that this evidence is ambiguous; the cutmarks supposedly could have resulted from hominids butchering fully fleshed carcasses\textsuperscript{21} or from hominids removing from the bones desiccated, tightly adhering scraps of meat, which commonly survive carcass consumption by carnivores.\textsuperscript{12,46,48} It was apparent that a more robust, experimentally and observationally controlled framework of cutmark frequency and distribution
in these different scenarios was needed.80

This work was carried out in two stages by Domínguez-Rodrigo. The first stage of research focused on recording patterns of the anatomical location of flesh scraps on medium-sized (150 to 350 kg) ungulate carcasses that had been killed, consumed, and then abandoned by large felids (lions).81 Domínguez-Rodrigo concentrated on medium-sized carcasses because remains from these ungulates make up the majority of large mammal fossils recovered in East African Plio-Pleistocene archeofaunas.18,24,44 The results of this stage of research demonstrated that lions, as initial carcass consumers, rarely leave much flesh on a carcass. When adhering flesh scraps were present, they occurred most frequently along the neck. Nearly 90% of meat scraps observed on limb bones occurred on the proximal and distal epiphysial and metaphysial sections of those bones. An important point is that no midshaft sections of any upper limb bone (humerus and femur) retained meat scraps.81

These results helped to contextualize the relevance of cutmark location in Plio-Pleistocene archeofaunas. Cutmarks observed on those sections of bones that are completely defleshed by primary carnivore consumers (for example, limb-bone midshaft portions, especially those portions on upper limb bones) likely reflect early access to carcasses by hominids, a behavior that is inconsistent with passive scavenging.80,82 Thus, it is apparent that accurate reporting of cutmark location per bone section is vital to inferences of the timing of hominid access to large mammal carcasses. In this regard, it is important to note Blumenschine reports that the highest incidence of cutmarks in the FLK Zinj assemblage occur on limb epiphysial specimens.50,52 However, a closer examination of these data reveals that many of these “limb epiphysis” specimens also preserve attached shaft sections, and it is on these shaft sections that the cutmarks actually occur.

Expanding on this referential framework, Domínguez-Rodrigo’s experimental research also demonstrated an inverse pattern of cutmark location when hominids gain early (fully fleshed) versus late (largely de-fleshed) access to ungulate carcasses.80,82 Humans with early access to carcasses impose the most cutmarks on upper limb bones (humerus and femur) because these bones support some of the largest muscle masses, one of the edible resources in the ungulate body that is of most interest to a hungry consumer. Fewer cutmarks occur on the slightly less meaty intermediate limb bones (radioulna and tibia); the fewest occur on the meat-deficient lower limb bones (metapodials). In addition, most cutmarks occur on the midshaft sections of all limb bones. Just the opposite pattern is observed when humans process largely defleshed, resource-poor carcasses consumed first by carnivores: Most cutmarks occur on lower limb bones, and very few occur on limb bone midshaft sections.

When this referential framework is applied to the FLK Zinj archeofauna, it bolsters Bunn’s18–21 early arguments that Plio-Pleistocene hominids at that site butchered carcasses carrying substantial amounts of meat. Bunn and Kroll25 summarized the conclusion of their landmark study of the FLK Zinj faunal assemblage as follows: “Cut marks are concentrated on the meaty limbs [i.e., upper and intermediate limb bones] of both smaller and larger animal carcasses. Sixty-two percent of all cut-marked bone specimens (30% of the total number of identified specimens and 39.2% of all cut-marked specimens from smaller animals) are from the meaty limb bones. A large majority of the cut marks on meaty limb bones occur on mid-shaft specimens rather than on or immediately adjacent to epiphyses. At least 61.3% of the cut marks on meaty limbs of smaller animals and at least 68.9% of the cut marks on meaty limbs of larger animals occur on shaft specimens, and these values are generous underestimates.”

Blumenschine’s hypothesis that Olduvai hominids operated as passive scavengers with a focus on marrow extraction from bones already defleshed by carnivores clearly is not supported by the combined work of Bunn17–21,44,45 and Domínguez-Rodrigo.80–82 This incongruity suggests that the pioneering experimental work carried out by Blumenschine and his colleagues to model carnivore and hominid influence in the FLK Zinj archeofauna lacked consideration of some crucial variables.

It is relevant to note here that Potts26 has documented a significant number of complete bones (9% to 10% of the total minimum number of elements) in most archeological sites in Bed I, Olduvai, including FLK Zinj. Given that hyena ravaging has also been documented at these sites,50,53 it is likely that the original number of complete bones was even higher immediately following abandonment by hominids.57 These points contradict archeologically detectable expectations of a passive scavenging strategy by hominids who were focused specifically on marrow exploitation. If hominids were forced to concentrate their carcass-foraging activities on marrow acquisition, it seems unlikely that they would transport marrow-containing limb bones to these Bed I sites and then choose not to break open a large percentage of them.

An additional point of evidence contradictory to the passive scavenging model is the relative abundance of axial bone specimens as measured by both the number of identified specimens and the minimum number of elements recovered in most Olduvai sites, including FLK Zinj. That site preserves more than 800 axial specimens (30% of the total number of identified specimens and 17.5% of the total minimum number of elements57). Experiments by Marean and his colleagues and by others50,57 have demonstrated that in simulated archeological sites hyenas preferentially destroy axial elements abandoned by hominids after defleshing. It thus seems that the significant sur-
vival of axial elements in early Olduvai sites attests to their even greater number before the affects of hyena ravaging. By extension, it can be inferred that hominids were transporting complete ungulate carcasses or axial sections of them (a portion of the carcass which, importantly, is devoid of marrow but very fleshy) to sites. These behaviors are consistent with early access to fully fleshted carcasses.

Finally, there is an additional piece of evidence that hominids were not passive marrow-scavengers. Indeed, this evidence indicates marrow abandonment by hominids. Blumenschine\textsuperscript{50} and Selvaggio\textsuperscript{55} demonstrated experimentally that the defleshing of limb bones from medium-sized ungulate carcasses by carnivores usually produces tooth marks on an average of 80\% of all recovered midshaft specimens. This percentage is consistent in cases in which carnivores deflesh and demarrow bones and in cases in which they simply deflesh carcasses, abandoning the marrow. The percentage of tooth-marked midshaft limb-bone sections from ungulate carcasses of comparable size in the FLK Zinj archeofauna (57\%) is outside the 95\% confidence interval of those experiments in which human defleshing and demarrowing of all the bones was followed by subsequent carnivore ravaging.\textsuperscript{50,57}

This disjunction suggested that hominids may have transported carcasses and parts of carcasses to early archaeological sites, where they then defleshed them, but demarrowed only a portion of the total limb-bone subassemblage. This scenario was modeled experimentally with a resulting toothmark pattern strikingly similar to that documented in the FLK Zinj archeofauna.\textsuperscript{82} This indicates that carnivore ravaging of the FLK Zinj fauna was not restricted to just demarrowed bones broken open by hominids.\textsuperscript{82} A similar pattern of limited marrow exploitation by hominids, rather than an obligate focus on this activity, is reflected in several other Early Stone Age archeofaunas. At sites such as FLK North 6 (Olduvai Gorge, Tanzania) and GaJi 5 (Koobi Fora, Kenya), as well as surface finds of isolated specimens from the GaJi area that are penecontemporaneous with the GaJi 5 site, many complete large mammal bones exhibit cutmarks, but were not demarrowed (that is, they are unbroken).\textsuperscript{18,44,83}

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Figure 2. Tooth-mark distribution according to limb bone section. Epiphyseal sections are highly tooth-marked irrespective of the type of carnivore access to ungulate carcasses. Midshaft sections show a high contrast according to whether carnivores have primary or secondary access to carcasses. Tooth-mark distributions in the archeofaunas indicate that carnivores were predominately secondary consumers of carcass parts at these early sites. Data from Blumenschine84 for FLK Zinj and the experimental samples, and Domínguez-Rodrigo84,86 for FxJj 50 and the ST site complex.

procurement and use. Putting aside differences, one of the most positive aspects of the hunting-versus-scavenging debate has been the valuable theoretical, methodological, and analytical contributions to zooarchaeology and taphonomy made by participants on both sides of that debate. With that said, it seems that while the debate will likely never be “resolved,” we will only come closer to consensus by expanding the basic archaeological dataset relevant to issues of early hominid carcass foraging.

For this reason, researchers have begun to apply the aforementioned actualistically derived models to assemblages other than FLK Zinj, but of roughly similar ages to that site. For example, the referential frameworks we have discussed have recently been applied to the c.1.6 Ma archeofauna from FxJj 50 (Koobi Fora, Kenya).84 As with the FLK Zinj fossil assemblage, the taphonomic data generated on the FxJj 50 accumulation suggest early access by hominids to the fully fleshed carcasses of large ungulates, and not passive scavenging. Most cutmarks in the FxJj 50 archeofauna occur on upper and intermediate limb bones and, further, most occur on the midshaft sections of limb bones. Tooth-mark frequencies in the assemblage are very low, with fewer limbbone midshaft sections preserving tooth marks than in experimental assemblages in which carcasses were defleshed by carnivores only. In addition, other broadly contemporaneous sites that show similar evidence of early access to large mammal carcasses by hominids include BK (c. 1.2 Ma), Bed II, Olduvai (Tanzania)65 and the ST site complex (c. 1.5 Ma), Peninj (Tanzania)66 (Figures 1 and 2.)

We agree with previous researchers such as Bunn that avenues of early access to large mammal carcasses by hominids were necessarily hunting and/or “power scavenging,” “the aggressive, confrontational driving away of primary predators or primary scavengers at kills.”67,88 Just a few of the factors that are likely to have mediated which of these two options, hunting or power scavenging, hominids engaged in any particular instance include, for each actor in the hominid-prey animal—carnivore-competitor dynamic: body size, strength, disposition, and group size. In, addition, the use of tools as weaponry by hominids, either for dispatching prey or fending off carnivore competitors, would surely factor into any carcass-acquisition strategy those hominids adopted. The important point is that the preponderance of taphonomic data generated in analyses of Plio-Pleistocene archeofaunas from East Africa supports the idea that it was these active types of carcass foraging in which hominids engaged most regularly.

This does not suggest that hominids never passively scavenged abandoned carnivore kills or naturally occurring carcasses. Passive scavenging is part of a flexible, wide-based foraging strategy used by modern hunter-gatherers86–89 and, though more rarely, by the closest living relative of humans, the chimpanzee.90 However, because taphonomic signatures of passive scavenging are not apparent or are obliterated by dominant taphonomic signatures indicating early hominid access to carcasses, it seems that passive scavenging was a less regular and less important part of hominid carcass foraging in the Plio-Pleistocene than were hunting and/or power scavenging. Also lacking support upon current examination of the Plio-Pleistocene zooarchaeological record in East Africa are elaborations of the passive scavenging model. For instance, the suggestion that hominids passively obtained partially fleshed ungulate carcasses through theft of temporarily abandoned, tree-stored leopard kills,91 which thus accommodates cutmark evidence within the passive scavenging model, is actually contradicted by examination of the FLK Zinj archeofauna. Cutmark patterns on the ungulate bones of prey of the body sizes preferred by leopards suggest that hominids had early access even to those carcass portions initially defleshed in the leopard feeding sequence.92 Similarly, the plausible hypothesis that hominids obtained carcasses in the wake of catastrophic events such as mass drownings of wildebeest herds93 still remains un-
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