Early Hominid Hunting and Scavenging: A Zooarcheological 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 hominid 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 hominid life ways, commonly known as the "Home Base" or "Food Sharing" model, was developed most fully by Glynn Isaac.[1–4] As Bunn and Stanford[5] emphasized, this model was greatly influenced by a paradigm that coalesced between 1966 and 1968, referred to as "Man the Hunter."[6]

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,[7–9] but rather was a scientifically couched commentary on a preoccupation by some male researchers with the assumed predatory nature of male early hominids.[10,11] 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*.[12–15]

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 manufacture. 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.[16–23] (We do note that the "Central Place Forag-ing" model was not necessarily a reaction to the "Obligate Marginal Scavenger" model, even though Isaac's[16] "Central Place Foraging" model was formally published in 1983, two years after Binford's[12] book *Bones: Ancient Men and Modern Myths*. As early as 1981, Isaac[24,25] 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.[26] 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.[27]

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.[28] Just as modern chimpanzee nest sites are recognizable by dung, hair, and modification of trees, so are

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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 founda-

tion 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 White[33]

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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 ethnoarcheological 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 ap-

plications 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 interpretive 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 limbs[16–21,45] 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, Blumenschine[48–53] 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 archeofaunas,[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 actualistically derived models of multiple-pattern faunal assemblages,[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.[61–78]

BONE SURFACE MODIFICATIONS AND THE UTILITY OF MULTIPLE-PATTERN MODELS

The multiple-pattern models of archeofauna 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.[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 archeofaunas. 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 commonsen-

sical. 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.[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.[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 (radioulna 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.[50,57]

The FLK *Zinj* archeofauna, because of its finely preserved bone surfaces, was a prime assemblage in which to apply this referential framework.[52] Blumenschine,[52] Selvaggio,[55,56] and Capaldo[57–60] all concluded that this large fossil assemblage (containing more than 3,500 identifiable bone specimens,[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 felid 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.[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[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[21] or from hominids removing from the bones desiccated, tightly adhering scraps of meat, which commonly survive carcass consumption by carnivores.[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 epiphyseal and metaphyseal 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 epiphysis 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

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bolsters Bunn's[18–21] early arguments that Plio-Pleistocene hominids at that site butchered carcasses carrying substantial amounts of meat. Bunn and Kroll[21] 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 from smaller animals and 39.2% of all cut-marked specimens from larger 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 Bunn[17–21,44,45] 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 Potts[26] 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 elements[57]). Experiments by Marean and his colleagues[47] and by others[50,57] have demonstrated that in simulated archeological sites hyenas preferentially destroy axial elements abandoned by hominids after defleshing. It thus seems that the significant sur-
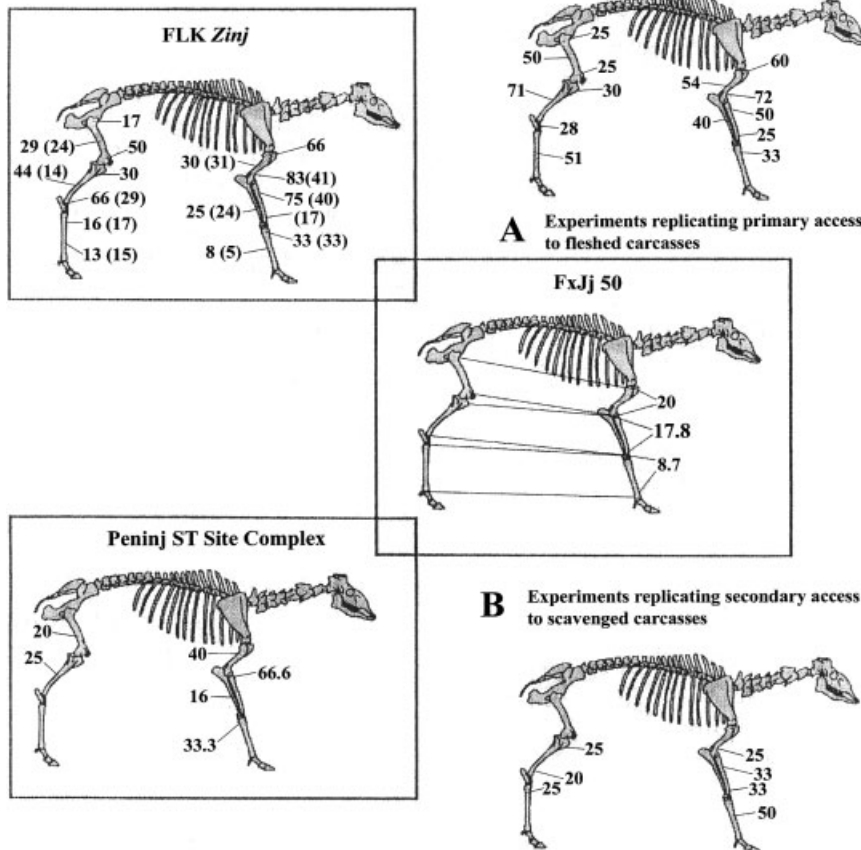
Figure 1. Distribution of cutmark percentages on limb bones. Note the contrast between experiments replicating primary and secondary access to ungulate carcasses by humans. All analyzed archeofaunal sites (FLK *Zinj*, FxJj 50, and ST site complex) show highly cutmarked meat-bearing bones. Most cutmarks on those bones are preserved on midshafts. These observations indicate early hominid access to fully fleshed ungulate carcasses at these sites. Values for FLK *Zinj* are for smaller ungulate carcasses (indicated outside the parentheses) and larger ungulate carcasses (indicated parenthetically). Data from Bunn and Kroll[21] for FLK *Zinj* and Domínguez-Rodrigo[80,84,86] for the other sites and experimental samples.

fleshed them, but demarrowed only a portion of the total limb-bone subassemblage. This scenario was modeled experimentally with a resulting tooth-mark pattern strikingly similar to that documented in the FLK *Zinj* archeofauna.[82] This indicates that carnivore ravaging of the FLK *Zinj* fauna was not restricted to just demarrowed bones broken open by hominids.[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

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the GaJi 5 site, many complete large mammal bones exhibit cutmarks, but were not demarrowed (that is, they are unbroken).[18,44,83]

NEW DIRECTIONS IN DETERMINING THE CARCASS FORAGING STRATEGIES USED BY PLIO-PLEISTOCENE HOMINIDS: EXPANDING SAMPLES AND TECHNIQUES

By the end of the 1990s, no clear consensus in paleoanthropology had emerged from the spate of actualistic work conducted during the previous twenty years on early hominid carcass
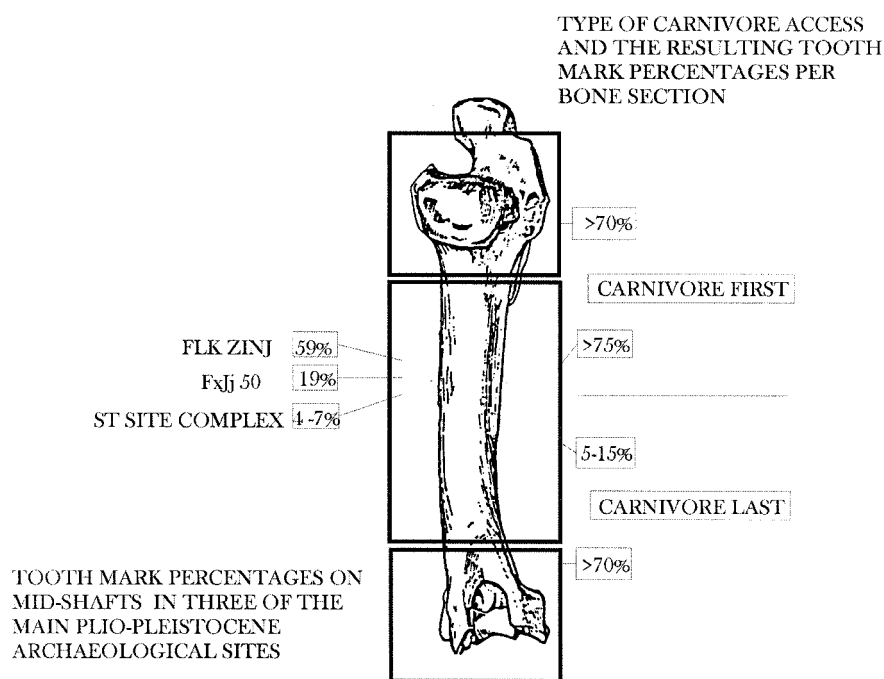
vival of axial elements in early Olduvai sites attests to their even greater number before the affects of hyena ravaging. By extension, it can be inferred that hominids were transporting complete ungulate carcasses or axial sections of them (a portion of the carcass which, importantly, is devoid of marrow but very fleshy) to sites. These behaviors are consistent with early access to fully fleshed 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[50] and Selvaggio[55] demonstrated experimentally that the defleshing of limb bones from medium-sized ungulate carcasses by carnivores usually pro-

duces 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 carnivores were the primary agents of carcass defleshing and those in which human defleshing and demarrowing of all the bones was followed by subsequent carnivore ravaging.[50,57]

This disjunction suggested that hominids may have transported carcasses and parts of carcasses to early archeological sites, where they then de-

TYPE OF CARNIVORE ACCESS
AND THE RESULTING TOOTH
MARK PERCENTAGES PER
BONE SECTION

>70%

CARNIVORE FIRST

FLK ZINJ 59%
FxJj 50 19%
ST SITE COMPLEX 4-7%

>75%

5-15%

CARNIVORE LAST

>70%

TOOTH MARK PERCENTAGES ON
MID-SHAFTS IN THREE OF THE
MAIN PLIO-PLEISTOCENE
ARCHAEOLOGICAL SITES

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 Blumenschine[52] for FLK *Zinj* and the experimental samples, and Domínguez-Rodrigo[84,86] 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 zooarcheology 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 archeological 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 limb-bone 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)[85] and the ST site complex (c. 1.5 Ma), Peninj (Tanzania)[86] (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."[87,88] Just a few of the factors that are likely to have mediated which of these two options, hunt-

ing 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-gatherers[36–39,89] 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 zooarcheological 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 herds[93] still remains un-

supported archeologically, taking into consideration the range of species and age profiles represented in early sites as compared to distributions of those variables observed in assemblages formed in comparable modern catastrophes.

Thus, in summary, the preponderance of zooarcheological data indicate that hominids in East Africa were gaining regular access to largely fleshed ungulate carcasses and were exploiting these carcasses fully for meat and intramuscular fat, with less emphasis on marrow harvesting. Although continued work on newly recovered Plio-Pleistocene archeofaunas and innovative actualistic research hold the potential to modify this interpretation of the carcass-foraging capabilities of early hominids, scenarios of hominids as passive scavengers, relegated to the role of marrow scroungers, are not currently supported.

REFERENCES

1 Isaac GLI. 1971. The diet of early man: aspects of archaeological evidence from Lower and Middle Pleistocene sites in East Africa. World Archaeol 2:279–298.

2 Isaac GLI. 1978. The food-sharing behavior of protohuman hominids. Sci Am 238:90–108.

3 Isaac GLI. 1984. The archaeology of human origins: studies of the Lower Pleistocene in East Africa, 1971–1981. In: Wendorf F, Close AE, editors. Advances in world archaeology, vol. 3. Orlando: Academic Press. p 1–87.

4 Leakey M. 1971. Olduvai Gorge, vol. 3. Excavations in Bed I and II, 1960–1963. Cambridge: Cambridge University Press.

5 Bunn HT, Stanford CB. 2001. Conclusions: research trajectories on hominid meat-eating. In: Stanford CB, Bunn HT, editors. Meat-eating and human evolution. Oxford: Oxford University Press. p 350–359.

6 Lee RB, DeVore I, editors. 1968. Man the hunter. Chicago: Aldine de Gruyter.

7 Tanner NM. 1979. Gathering by females: the chimpanzee model revisited and the gathering hypothesis. In: Kinzey WG, editor. The evolution of human behavior: primate models. New York: SUNY Press. p 3–27.

8 Tanner NM. 1981. On becoming human. Cambridge: Cambridge University Press.

9 Zihlman AL. 1981. Women as shapers of human adaptation. In: Dahlberg F, editor. Woman the gatherer. New Haven: Yale University Press. p 75–120.

10 Stanford CB, Allen JS. 1991. Strategic storytelling: current models of human behavioral evolution. Curr Anthropol 32:58–61.

11 Stanford CB, Bunn HT. 2001. Introduction. In: Stanford CB, Bunn HT, editors. Meat-eating and human evolution. Oxford: Oxford University Press. p 3–10.

12 Binford LR. 1981. Bones: ancient men and modern myths. New York: Academic Press.

13 Binford LR. 1985. Human ancestors: changing views of their behavior. J Anthropol Archaeol 4:292–327.

14 Binford LR. 1986. Response to Bunn and Kroll. Curr Anthropol 27:444–446.

15 Binford LR. 1988. The hunting hypothesis, archaeological methods and the past. Yearbook Phys Anthropol 30:1–9.

16 Isaac GLI. 1983. Bones in contention: competing explanations for the juxtaposition of Early Pleistocene artifacts and faunal remains. In: Clutton-Brock J, Grigson C, editors. Animals and archaeology, vol. 1: Hunters and their prey. Oxford: British Archaeological Reports International Series 163. p 3–19.

17 Bunn HT. 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora, Kenya. Nature 291:574–577.

18 Bunn HT. 1982. Meat-eating and human evolution: studies on the diet and subsistence patterns of Plio-Pleistocene hominids in East Africa. Ph.D. dissertation. University of California, Berkeley.

19 Bunn HT. 1983. Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. In: Clutton-Brock J, Grigson C, editors. Animals and archaeology, vol. 1: Hunters and their prey. Oxford: British Archaeological Reports International Series, 163. p 21–30.

20 Bunn HT. 1991. A taphonomic perspective on the archaeology of human origins. Ann Rev Anthropol 20:433–467.

21 Bunn HT, Kroll EM. 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. Curr Anthropol 27:431–452.

22 Kroll EM. 1997. Lithic and faunal distributions at eight archaeological excavations. In: Isaac GLI, Isaac B, editors. Koobi Fora Research Project, vol. 5: Plio-Pleistocene archaeology. Oxford: Clarendon Press. p 459–543.

23 Kroll EM, Isaac GLI. 1984. Configurations of artifacts and bones at early Pleistocene sites in East Africa. In: Hietala HJ, editor. Intrasite spatial analysis in archaeology. Cambridge: Cambridge University Press. p 4–31.

24 Isaac GLI. 1981. Archaeological tests of alternative models of early hominid behaviour: excavation and experiments. Philos Trans R Soc London 292:177–188.

25 Isaac GLI. 1981. Stone Age visiting cards: approaches to the study of early land use patterns. In: Hodder I, Isaac GLI, Hammond N, editors. Patterns of the past. Cambridge: Cambridge University Press, p 205–257.

26 Potts R. 1988. Early hominid activities at Olduvai. New York: Aldine de Gruyter.

27 Blumenschine RJ, Cavallo JA, Capaldo SD. 1994. Competition for carcasses and early hominid behavioral ecology: a case study and a conceptual framework. J Hum Evol 27:197–213.

28 Sept JM. 1992. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. Curr Anthropol 33:187–207.

29 Schick K, Toth N. 1993. Making silent stones speak: human evolution and the dawn of technology. New York: Simon and Schuster.

30 Domínguez-Rodrigo M. 1994. El origen del comportamiento humano. Madrid: Tipo.

31 Rose L, Marshall F. 1996. Meat eating, hominid sociality, and home bases revisited. Curr Anthropol 37:307–338.

32 O'Connell JF. 1997. On Plio-Pleistocene archaeological sites and central places. Curr Anthropol 38:86–88.

33 White TE. 1952. Observations on the butchering technique of some aboriginal peoples, 1. Am Antiquity 17:337–338.

34 Perkins D, Daly P. 1968. A hunters' village in Neolithic Turkey. Sci Am 219:97–106.

35 Binford LR. 1978. Nunamiut ethnoarchaeology. New York: Academic Press.

36 Bunn HT, Kroll EM, Bartram, LE. 1988. Variability in bone assemblage formation from Hadza hunting, scavenging and carcass processing. J Anthropol Archaeol 7:412–457.

37 Bunn HT. 1993. Bone assemblages at base camps: a further consideration of carcass transport and bone destruction by the Hadza. In: Hudson J, editor. From bones to behavior: ethnoarchaeological and experimental contributions to the interpretation of faunal remains. Carbondale: Southern Illinois University Press. p 156–168.

38 O'Connell JF, Hawkes K, Blurton-Jones N. 1988. Hadza hunting, butchering and bone transport and their archaeological implications. J Anthropol Res 44:113–161.

39 O'Connell JF, Hawkes K, Blurton-Jones N. 1990. Reanalysis of large mammal body part transport among the Hadza. J Archaeol Sci 17:301–316.

40 O'Connell JF, Hawkes K, Blurton Jones N. 1992. Patterns in the distribution, site structure and assemblage composition of Hadza kill-butchering sites. J Archaeol Sci 19:319–345.

41 Bartram LE. 1993. An ethnoarchaeological analysis of Kua San (Botswana) bone food refuse. Ph.D. dissertation, University of Wisconsin-Madison.

42 Bartram LE. 1993. Perspectives on skeletal part profiles and utility curves from Eastern Kalahari ethnoarchaeology. In: Hudson J, editor. From bones to behavior: ethnoarchaeological and experimental contributions to the interpretations of faunal remains. Carbondale: Southern Illinois University Press. p 115–137.

43 Gifford-Gonzalez D. 1989. Ethnographic analogues for interpreting modified bones: some cases from East Africa. In: Bonnichsen R, Sorg M, editors. Bone modification. Oron, ME: Center for the Study of the First Americans. p 179–246.

44 Bunn HT. 1997. The bone assemblages from the excavated sites. In: Isaac GLI, Isaac B, editors. Koobi Fora Research Project, vol. 5: Plio-

Pleistocene archaeology. Oxford: Clarendon Press. p 402–444.

45 Bunn HT, Ezzo JA. 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. J Archaeol Sci 20:365–398.

46 Shipman P. 1986. Scavenging or hunting in early hominids: theoretical frameworks and tests. Am Anthropol 88:27–43.

47 Marean CW, Spencer LM, Blumenschine RJ, Capaldo SD. 1992. Captive hyaena bone choice and destruction, the schlepp effect and Olduvai archaeofaunas. J Archaeol Sci 19:101–121.

48 Blumenschine RJ. 1986. Response to Bunn and Kroll. Curr Anthropol 27:446.

49 Blumenschine RJ. 1986. Early hominid scavenging opportunities: implications of carcass availability in the Serengeti and Ngorongoro ecosystems. Oxford: British Archaeological International Series. 283.

50 Blumenschine RJ. 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. J Archaeol Sci 15:483–502.

51 Blumenschine RJ. 1991. Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. Philosophical Trans R Soc (London) 334:211–221.

52 Blumenschine RJ. 1995. Percussion marks, tooth marks and the experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus,* Olduvai Gorge, Tanzania. J Hum Evol 29:21–51.

53 Blumenschine RJ, Marean CW. 1993. A carnivore's view of archaeological bone assemblages. In: Hudson J, editor. From bones to behavior: ethnoarchaeological and experimental contributions to the interpretation of faunal remains. Carbondale: Southern Illinois University Press. p 273–300.

54 Potts R, Shipman P. 1981. Cutmarks made by stone tools from Olduvai Gorge, Tanzania. Nature 291:577–580.

55 Selvaggio MM. 1994. Identifying the timing and sequence of hominid and carnivore involvement with Plio-Pleistocene bone assemblages from carnivore tooth marks and stone-tool butchery marks on bone surfaces. Ph.D. dissertation, Rutgers University, New Brunswick, NJ.

56 Selvaggio MM. 1994. Carnivore tooth marks and stone tool butchery marks on scavenged bone: archaeological implications. J Hum Evol 27:215–227.

57 Capaldo SD. 1995. Inferring hominid and carnivore behavior from dual-patterned archaeological assemblages. Ph.D. dissertation, Rutgers University, New Brunswick, NJ.

58 Capaldo SD. 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. J Hum Evol 33:555–597.

59 Capaldo SD. 1998. Simulating the formation of dual-patterned archaeofaunal assemblages with experimental control samples. J Archaeol Sci 25:311–330.

60 Capaldo SD. 1998. Methods, marks and models for inferring hominid and carnivore behavior. J Hum Evol 35:323–326.

61 Brain CK. 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. Sci Pap Namib Desert Res Station 32:1–11.

62 Brain CK. 1969. The contributions of Namib Desert Hottentots to an understanding of australopithecine bone accumulations. Sci Pap Namib Desert Res Station 29:13–22.

63 Binford LR, Bertram JB. 1977. Bone frequencies—and attritional processes. In: Binford LR, editor. For theory building in archaeology. New York: Academic Press, p 77–153.

64 Grayson DH. 1989. Bone transport, bone destruction, and reverse utility curves. J Archaeol Sci 16:643–652.

65 Lyman RL. 1982. The taphonomy of vertebrate archaeofaunas: bone density and differential survivorship of fossil classes. Ph.D. dissertation, University of Washington.

66 Lyman RL. 1984. Bone density and differential survivorship of fossil classes. J Anthropol Archaeol 3:259–299.

67 Lyman RL. 1992. Anatomical considerations of utility curves in zooarchaeology. J Archaeol Sci 19:7–22.

68 Lyman RL. 1993. Density-mediated attrition of bone assemblages: new insights. In: Hudson J, editor. From bones to behavior: ethnoarchaeological and experimental contributions to the interpretation of faunal remains. Carbondale: Southern Illinois University Press. p 324–341.

69 Lyman RL. 1994. Vertebrate taphonomy. Cambridge: Cambridge University Press.

70 Lyman RL, Houghton LE, Chambers AL. 1992. The effect of structural density on marmot skeletal part representation in archaeological sites. J Archaeol Sci 19:557–573.

71 Kreutzer LA. 1992. Bison and deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas. J Archaeol Sci 19:271–294.

72 Elkin DC. 1995. Volume density of South American camelid skeletal parts. Int J Osteoarchaeol 5:29–37.

73 Lam YM, Chen X, Marean CW, Frey CJ. 1998. Bone density and long bone representation in archaeological faunas: comparing results from CT and photon densitometry. J Archaeol Sci 25:559–570.

74 Lam YM, Chen X, Pearson OM. 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. Am Antiquity 64:343–362.

75 Bartram LE, Marean CW. 1999. Explaining the "Klasies Pattern": Kua ethnoarchaeology, the Die Kelders Middle Stone Age archaeofauna, long bone fragmentation and carnivore ravaging. J Archaeol Sci 26:9–29.

76 Stahl PW. 1999. Structural density of domesticated South American camelid skeletal elements and the archaeological investigation of prehistoric Andean ch'arki. J Archaeol Sci 26:1347–1368.

77 Pavao B, Stahl PW. 1999. Structural density assays of leporid skeletal elements with implications for taphonomic, actualistic and archaeological research. J Archaeol Sci 26:53–66.

78 Pickering TR, Carlson KJ. 2002. Baboon bone mineral densities: implications for the taphonomy of primate skeletons in South African cave sites. J Archaeol Sci 29:883–896.

79 Oliver JS. 1994. Estimates of hominid and carnivore involvement in the FLK *Zinjanthropus* fossil assemblage: some socioecological implications. J Hum Evol 27:267–294.

80 Domínguez-Rodrigo M. 1997. Meat-eating by early hominids at the FLK 22 *Zinjanthropus* site, Olduvai Gorge, Tanzania: an experimental approach using cut mark data. J Hum Evol 33:669–690.

81 Domínguez-Rodrigo M. 1999. Flesh availability and bone modification in carcasses consumed by lions. Palaeogeogr Palaeoclimatol Palaeoecol 149:373–388.

82 Domínguez-Rodrigo M. 1999. Meat-eating and carcass procurement at the FLK *Zinj* 22 site, Olduvai Gorge (Tanzania): a new experimental approach to the old hunting-versus-scavenging debate. In: Ullrich H, editor. Lifestyles and survival strategies in Pliocene and Pleistocene hominids. Schwelm (Germany): Edition Archaea. p 89–111.

83 Bunn HT. 1994. Early Pleistocene hominid foraging strategies along the ancestral Omo River at Koobi Fora, Kenya. J Hum Evol 27:247–266.

84 Domínguez-Rodrigo M. 2002. Hunting and scavenging in early humans: the state of the debate. J World Prehist 16:1–56.

85 Monahan CM. 1996. New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominid behavior in the Early Pleistocene. J Hum Evol 31:93–128.

86 Domínguez-Rodrigo M, de Luque L, Alcalá L, de la Torre Sainz I, Mora R, Serrallonga J, Medina V. 2002. The ST site complex at Peninj, West Lake Natron, Tanzania: implications for early hominid behavioral models. J Archaeol Sci 29:639–665.

87 Bunn HT. 1996. Response to Rose and Marshall. Curr Anthropol 37:321–323.

88 Bunn HT. 2001. Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene *Homo*. In: Stanford CB, Bunn HT, editors. Meat-eating and human evolution. New York: Oxford University Press. p 199–218.

89 O'Connell JF, Hawkes K, Blurton-Jones N. 1988. Hadza scavenging: implications for Plio-Pleistocene hominid subsistence. Curr Anthropol 29:356–363.

90 Hasegawa T, Hiraiwa M, Nishida T, Takasaki H. 1983. New evidence on scavenging behavior in wild chimpanzees. Curr Anthropol 24:231–232.

91 Cavallo JA, Blumenschine RJ. 1989. Tree-stored leopard kills: expanding the hominid scavenging niche. J Human Evol 18:393–399.

92 Cavallo JA. 1997. A re-examination of Isaac's central-place foraging hypothesis. Ph.D. dissertation, Rutgers University, New Brunswick, NJ.

93 Capaldo SD, Peters CR. 1995. Skeletal inventories from wildebeest drownings at Lakes Masek and Ndutu in the Serengeti ecosystem of Tanzania. J Archaeol Sci 22:385–408.