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Hominid Carnivory and Foraging Strategies, and the Socio-Economic Function of Early Archaeological Sites [and Discussion]

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Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites

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SUMMARY

New evidence for the tissue types exploited by early hominids from carcasses possibly acquired through scavenging is derived from the larger mammal bone assemblages from FLK I, level 22 (*Zinjanthropus* floor), and FLKN levels 1 and 2 from Bed I, Olduvai Gorge, Tanzania. Published skeletal part profiles from the two archaeological sites are evaluated using (i) modern observations on the sequence by which carnivores consume carcass parts in order to assess the timing of hominid access to carcasses, and (ii) measurements of flesh and marrow yields to assess the tissue types sought and acquired. These results suggest that the maximization of marrow (fat) yields, not flesh (protein) yields, was the criterion shaping decisions about carcass processing. Because of evidence for density-dependent destruction of some flesh-bearing parts by scavengers of the hominid-butchered assemblages, however, it is uncertain whether carcass parts were transported and acquired by hominids in a largely defleshed condition. The results on tissue types acquired are combined with a discussion of predation risk, feeding competition and the equipment needs of carcass processing in an attempt to identify archaeological test implications of competing hypotheses for the socio-economic function of the earliest archaeological sites.

1. INTRODUCTION

A Stone Age archaeologist may envy the ethologist who can observe diet and foraging behaviour through binoculars rather than by examining the types and locations of food residues and processing tools their subjects leave behind. The earliest, two-million-year-old archaeological evidence for hominid diet and foraging comes from a handful of sites containing flaked stone artifacts and fragmented bones of diverse vertebrate species. Decoding these fossilized traces of behaviour must precede investigation of issues in evolutionary ecology that can engross one studying living primates from the start. The bones at these sites have passed through many taphonomic filters from the time an animal died until its excavated remains are interpreted. These physical and biological filters, whose identification and joint effects are imperfectly understood, introduce many potential observational biases that conspire to distort, but hopefully not mask, the dietary and foraging signals contained in the bone remains.

None the less, the animal-food diet and foraging strategies of early hominids are central issues in palaeoanthropology. The quality of evidence for them is better than for most aspects of prehistoric adaptation. And, the opening lament aside, archaeological pursuit of this issue is important because comparative primate studies, although vital for defining primitive and uniquely derived components of human diet and foraging, cannot replace the fossil record for revealing the exact courses and circumstances of human subsistence evolution (Isaac 1968). The earliest archaeological record is most pertinent because it testifies to the emergence of a unique modification to generalized primate omnivory that involved stone-tool-mediated consumption of larger mammals, acquired possibly through corporate rather than individualistic foraging (Isaac 1978).

Isaac (e.g. 1978, 1980, 1981) was the first archaeologist to systematically explore the relationship between hominid diet and foraging behaviour. His goal was to provide fossil evidence for his home base – food sharing model of the socio-economic function of Plio-Pleistocene sites from Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. Later relabelled as central place foraging (Isaac 1983), Isaac's socio-economic model maintained that meat and marrow from larger mammals, whether acquired by hunting or scavenging, were obtained in a corporate manner and in sufficiently large packets to sustain a system of food reciprocity. Accordingly, early archaeological sites represent places from which hominids practised radiative foraging on a daily basis: plant-gathering and animal-food-acquiring sub-groups procured food in surplus quantities and returned it to the site for intentional or *de facto* sharing among group members. Among other evidence, Isaac used the presence of stone tool cut marks on meat-bearing limb bones (see Bunn *et al.* 1980) to argue that meat from larger mammals was the central commodity of the food sharing system.

Binford (1981, 1986, 1988) countered Isaac's and later Bunn's (1986) position by arguing that hominids scavenged from the nutritionally marginal, mostly

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marrow, leftovers of carnivore prey. Although Bunn & Kroll (1986, 1988) have shown that the skeletal part data upon which Binford's interpretation was based produced flawed profiles, Binford (1985) maintained that hominids were engaged in minimal food transport and no sharing because carcass yields were too meagre to satisfy even an individual's hunger. Foraging was akin to the 'individualistic-feed-as-you-go' foraging (Isaac, 1983) of non-human primates, a strategy that can be referred to as routed foraging (Binford, 1984).

Others have added to the debate. Shipman (1983, 1986) argued from stone-tool cut mark data for an absence of carcass disarticulation by hominids (but see Bunn & Blumenschine (1986); Gifford-Gonzalez (1989); Lyman (1987)). This indicated to her 'an opportunistic foraging scavenging mode of life' (Shipman 1983) lacking food sharing and other characteristics of human hunting–gathering. Potts (1984) argued that hominids transported carcass parts, acquired through hunting and scavenging (Potts 1983), to caches of stone for butchery. The caches had been pre-established throughout the foraging range in anticipation of eventually finding a carcass nearby. Potts added that danger from carnivores drawn to a cache would render the sites servicable only as briefly visited carcass processing locales, and not home bases. On the basis of a study of modern scavenging opportunities from ungulates in the Serengeti region of Tanzania, Blumenschine (1986*a*, 1987) identified abandoned lion kills as potentially the most regular scavenging opportunity encountered by early hominids. Abandoned lion kills in riparian woodlands are predictably located and typically provide little flesh but mostly marrow and head contents; this yield was suggested to be too low either to finance transport or to sustain an active system of food sharing.

The crux of the debate between Issac and Binford on the socio-economic function of early archaeological sites is not whether hominids hunted or scavenged, but rather whether the nutritional yield (i.e. tissue types and amounts acquired) and regularity of carcass acquisition by hominids was adequate to promote food transport and sharing. Indeed, a range of potential scavenging opportunities for early hominids other than that from lion kills have been identified by Blumenschine (1986*a*, 1987), by Cavallo (Cavallo & Blumenschine 1989) from tree-stored leopard kills, and by Marean (1989; see also Blumenschine (1987)) from saber-tooth cat kills. These studies show that scavenging may have been a high-yield, low-risk, predictable source of animal foods for hominids.

Here, I attempt to make explicit linkages between carcass acquisition and foraging by hominids. The links are defined by various motivations and constraints on carcass part transport from a death site. These in turn serve to define the socio-economic function of early archaeological sites. One major link, as argued above, is the nutrient yield and availability of carcass parts acquired. I use direct determinations of marrow and flesh masses and naturalistic observations on carcass consumption by carnivores to interpret skeletal part data from the two largest and best reported Plio-Pleistocene archaeological bone assemblages. These sites are FLKI level 22 (the '*Zinjanthropus* floor'), and FLKN levels 1 and 2. Both date between 1.8 and 1.7 Ma from Bed I of Olduvai Gorge, Tanzania, and were deposited in fine-grained sediments near the shore of a shallow lake that occupied the Olduvai Basin (Leakey 1971). FLK Zinj contains 60000 plus bones, approximately 3350 of which can be identified to derive from a minimum of 48 larger mammal individuals (Bunn & Kroll 1986). FLKN 1/2 has 45 such individuals represented by 2274 identified bone specimens (Bunn 1986). Most larger mammal bones at both sites derive from species of the family Bovidae.

2. NUTRIENT YIELD AND CARCASS CONSUMPTION SEQUENCES

Skeletal part profiles have been used by archaeologists to address modes of carcass acquisition by hominids. Blumenschine (1986*b*) argued that the carcass consumption sequence, i.e. the order in which carcass parts are depleted of flesh and within-bone tissues (marrow, brain, etc.) by modern larger mammalian and avian carnivores, is the most appropriate model available for interpreting skeletal part profiles to these ends. So far it and alternative models (Binford

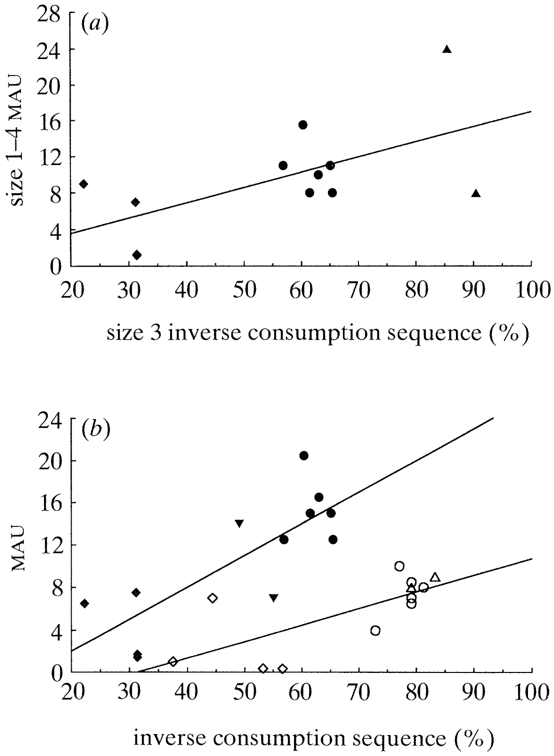

Figure 1. Carcass part availability and MAU representation at FLK Zinj (*a*) and FLKN 1/2 (*b*). Inverse consumption sequence values are based on Blumenschine (1986), and MAU values are from Bunn (1986) (see table 1). Open symbols, size 1 and 2 mammals; closed symbols, size 3 and 4 mammals. Diamonds, flesh from post-cranial axial parts; inverse triangles, flesh from head parts; circles, marrow from long bones; upright triangles, contents of head parts. Regression statistics: (*a*) $y = 0.17x+0.24$, $r = 0.61$, $p = 0.04$; (*b*) size 1 and 2 mammals, $y = 0.16x-4.9$, $r = 0.72$, $p = 0.008$; size 3 and 4 mammals, $y = 0.30x-3.9$, $r = 0.80$, $p = 0.002$.

Table 1. *Raw data used for analysis of skeletal part profiles*

(Skeletal parts used are those provided by Bunn (1986) for FLK Zinj. and FLKN 1/2. S12 = size 1 and 2; S34 = size 3 and 4 (see footnote a for definition of animal size groups).)

skeletal part	yield/g		inverse consumption sequence[e]		bulk density[g]	FLK ZINJ MAU[i]	FLKN 1/2 MAU[i]
	marrow[a]	flesh[b]	marrow	flesh			
head							
cranium					0.61[h]	8	16
S12	146.8[c]	303.3	83.8	45.8	—	—	9
S34	325[c]	1065.5	90.5	55.1	—	—	7
mandible					0.61	24	22
S12	10[d]	303.3	79.2	54.2	—	—	8
S34	10[d]	1065.5	85.6	49.1	—	—	14
post-cranial axial							
vertebrae					0.30	1.3	2.07
S12	—	6543.4	—	56.6[f]	—	—	0.33
S34	—	11507.3	—	31.4[f]	—	—	1.74
ribs					0.40	1.19	1.77
S12	—	7054.1	—	53.2	—	—	0.35
S34	—	18752.7	—	31.4	—	—	1.42
pelvis					0.49	9	7.5
S12	—	1596.0	—	37.5	—	—	1
S34	—	5185.4	—	22.3	—	—	6.5
scapula					0.49	7	14.5
S12	—	3000.4	—	44.4	—	—	7
S34	—	8239.8	—	31.2	—	—	7.5
long bones							
humerus					0.63	10	25
S12	19.96	1723.6	79.2	47.8	—	3	8.5
S34	48.08	4830.2	63.1	29.3	—	7	16.5
radius-ulna					0.68	11	22
S12	18.32	766.1	79.2	53.2	—	3	7
S34	67.26	1704.8	65.2	45.2	—	8	15
femur					0.57	11	16.5
S12	32.52	9384.2	72.9	33.3	—	4	4
S34	53.66	16053.5	56.9	22.2	—	7	12.5
tibia					0.74	15.5	30.5
S12	46.52	1340.6	77.1	41.7	—	6	10
S34	117.5	2557.2	60.4	36.6	—	9.5	20.5
metacarpal					0.72	8	19
S12	14.3	—	79.2	—	—	3	6.5
S34	27.7	—	65.5	—	—	5	12.5
metatarsal					0.74	8	23
S12	16.66	—	81.3	—	—	5	8
S34	26.34	—	61.5	—	—	3	15

[a] Long bone values are average adult wet masses of marrow in diaphyseal cavities (Blumenschine & Madrigal, in preparation). Size 1–2 based on two Thomson's gazelle, three Grant's gazelle, and two impala; size 3–4 based on five wildebeest. Whole-animal values are given (i.e. single bone yield is multiplied by 2 for paired parts) in keeping with use of MAU values for archaeological sites.

[b] Based on average adult male wet masses from Blumenschine & Caro (1986). Size 1–2 based on percent of total flesh mass for two Thomson's gazelle, two Grant's gazelle and two impala multiplied by the average total flesh mass (31919 g) for the Grant's gazelle and impala. Size 3–4 based on three wildebeest. Whole-animal values are given (i.e. single bone yield is multiplied by 2 for paired parts). Blumenschine & Caro's head flesh values are equally divided between cranium and mandible, whereas flesh yields for vertebrae are the sum of their neck flesh and lumbar flesh. Rib flesh includes thoracic vertebrae flesh.

[c] Based on brain mass (325 g) of one adult male wildebeest (size 3) equalling 0.46% of total flesh mass. Size 1–2 brain mass therefore = 31919 (total flesh mass) × 0.0046.

[d] Based on one subadult zebra (R. J. Blumenschine, unpublished data).

[e] Average percentage of parts encountered upon discovery of a carcass that remained with some flesh, marrow or other contents (see Blumenschine 1986). Values for size 3–4 based on consumption sequence for size 3 carcasses only.

[f] Average values for cervical vertebrae, lumbar vertebrae and rib cage.

[g] Based on Lyman's (1984) photondensitometer measurements for densest part of each bone sampled.

[h] Based on Lyman's (1984) value for the mandible, as cranium has similar density as the mandible in other studies cited by Lyman.

[i] From Bunn (1986, tables 2 and 4). Size-specific MAU are only available for long bones at FLK Zinj.

Table 2. *Correlation and regression statistics relating the inverse consumption sequence, yield of flesh and marrow parts, and bulk density to* MAU *values from FLK Zinj and FLKN 1/2*

(Values are Pearson's correlation coefficient (top), probability (middle), and the slope ± s.e. for the least squares regression line (bottom). The latter is not provided for bulk density. S12, size 1 and 2; S34, size 3 and 4; S14, size 1 to 4.)

	FLK Zinj.			FLKN 1/2		
	S12	S34	S14[a]	S12	S34	S14
inverse consumption sequence						
model IA						
post-cranial axial flesh,	—	—	0.61	0.71	0.56	—
head contents, long bone	—	—	0.04	0.008	0.06	—
marrow ($n = 12$ parts)	—	—	0.17 ± 0.07	0.16 ± 0.05	0.17 ± 0.07	—
model IB						
post-cranial axial flesh,	—	—	0.39	0.43	0.80	—
head flesh, long bone	—	—	0.21	0.16	0.002	—
marrow ($n = 12$ parts)	—	—	0.15 ± 0.11	0.09 ± 0.06	0.30 ± 0.07	—
model II						
flesh values only	—	—	0.38	−0.08	0.17	—
($n = 10$ parts)	—	—	0.28	0.83	0.64	—
	—	—	0.23 ± 0.20	−0.04 ± 0.17	0.10 ± 0.20	—
log yield (grams)						
long bone marrow	0.68	0.96	0.91	0.18	0.71	0.76
($n = 6$ or 12)	0.14	0.003	0.0001	0.73	0.11	0.004
	4.3 ± 2.4	8.9 ± 1.4	7.3 ± 1.0	1.9 ± 5.1	8.6 ± 4.3	13.2 ± 3.6
flesh, all parts	—	—	−0.67	−0.67	−0.49	—
($n = 10$)	—	—	0.04	0.03	0.15	—
	—	—	−95 ± 3.8	−4.7 ± 1.8	−6.8 ± 4.2	—
flesh, long bones	0.07	−0.63	0.23	−0.73	−0.61	0.03
($n = 4$ or 8)	0.93	0.37	0.59	0.27	0.40	0.94
	0.2 ± 2.1	−1.8 ± 1.5	1.2 ± 2.1	−4.0 ± 2.7	−4.7 ± 4.4	0.4 ± 4.9
bulk density						
all parts ($n = 12$)	—	—	0.56	0.82	0.88	—
	—	—	0.06	0.001	0.0001	—
long bones ($n = 6$)	0.44	−0.21	—	0.68	0.42	—
	0.38	0.68	—	0.14	0.40	—

[a] Uses size 3 values for inverse consumption sequence and log yield except for analyses restricted to long bones, where size-specific models are used.

1984; Potts 1983) have been applied to only a handful of Pleistocene bone assemblages.

The carcass consumption sequence is very regular for a wide range of carnivores (lions, cheetah, spotted hyena, vultures) and larger mammal carcass sizes (Blumenschine 1986*a*, *b*). In its regional expression the sequence proceeds from (i) hindquarter flesh to (ii) forequarter flesh, (iii) head flesh, (iv) hindlimb marrow, (v) forelimb marrow, and (vi) head contents (brain, and pulps of the mandible and cranium) (see also Haynes (1982)).

The regular sequence of carcass consumption has an energetic basis. The consumption sequence values for parts from medium-sized ungulates are significantly correlated with flesh mass. This suggests that carnivores are maximizing their rate of feeding by preferentially eating from skeletal units that offer the highest tissue yields (Blumenschine 1986*b*). The fundamental basis of the consumption sequence justifies the uniformitarian assumption that prehistoric mammalian carnivores consumed carcass parts in a similar order, and that the consumption sequence can be used to interpret skeletal part profiles at archaeological sites with regard to the timing of hominid access to carcasses. Specifically, if hominids had first access to a carcass (as in hunting), they should have acquired an anatomically even distribution of skeletal parts, or one skewed toward the highest yielding parts that are consumed early in the sequence. Late access to partially consumed carcasses (scavenging), on the other hand, should be characterized by the availability of food from parts consumed only in the latter part of the consumption sequence. The consumption sequence can be expressed in units that reflect the percentage of time I encountered a carcass part with some edible tissue remaining on or in it (i.e. the inverse consumption sequence). Hominid hunting is modelled by a negative relationship between a bone assemblage's skeletal part representation and the inverse consumption sequence, and scavenging by a positive one (Blumenschine 1986*b*; see, for example, figure 1).

3. YIELD AND AVAILABILITY OF SKELETAL PARTS AT FLK Zinj. AND FLKN 1/2

The abundance of different skeletal parts from FLK Zinj and FLKN 1/2 is expressed in Minimum Animal Units (MAU; Binford 1984), as determined by Bunn

(1986; Bunn & Kroll 1986). These values (table 1) are an expression of the minimum number of animals required to account for the skeletal parts present. If all individuals are represented by complete skeletons, the MAU values for each skeletal unit would be equal†. MAU values for all skeletal units are available for size 1–2 and size 3–4 mammals‡ for FLKN 1/2; published data on FLK Zinj permit such size discrimination only for long bone MAUS.

Skeletal part proportions at the two sites are uneven with respect to those in whole animals. The paucity of post-cranial axial parts, particularly ribs and vertebrae, may indicate the selective transport of long bones and heads from the death site to the archaeological site (Bunn 1986; Bunn & Kroll 1986). Alternatively, Marean *et al.* (1991) have shown quantitatively that the pattern is consistent with the preferential deletion of the uncommon parts by site scavengers after hominid butchery occurred. Here, I use the carcass consumption sequence to investigate whether the uneven skeletal part profiles might also be related to the differential availability of carcass foods at a death site.

Three consumption sequence models are used (table 2). Each is based on the alternative availability of edible tissues for those parts that bear flesh and contain either marrow (long bones) or other edible tissues (cranium and mandible). Models IA and IB reflect the standard availability of edible tissues from abandoned lion and cheetah kills (Blumenschine 1987), which, if not thoroughly defleshed (model IA), will retain flesh lastly on the head (model IB). Model II uses values for flesh only.

The best fit consumption sequence models for both sites (i.e. those with the highest Pearson's correlation coefficient) are models IA and IB, where significantly positive relationships are found; model II yields poorly correlated, statistically insignificant results (figure 1*a*, *b*, table 2). These results, particularly the significantly positive slopes of the regression equations, are consistent with scavenging of carcasses that had been largely defleshed before hominid access. The greater abundance at both sites of long bones and head parts compared to post-cranial axial flesh-bearing parts is therefore consistent with the high probability (large inverse consumption sequence value) of finding abandoned predator kills with defleshed long bones that still contain marrow, and head parts, which, if not remaining with flesh, still contain the brain and pulps.

The above indications of scavenging are supported by data on the flesh and marrow yields of bones at the two sites. Both assemblages show strong, significantly positive relationships between marrow yield and long bone MAUS (figure 2, table 2; Blumenschine & Madrigal, in preparation). These relationships are made more intriguing by the fact that small, size 1–2 long bones are in general less abundant that those of large mammals in a manner predicted by their lower marrow yield: for FLK Zinj, the least squares regression line describing the relationship for size 1–2 bones is very similar to that for size 3–4 bones. Further, the slopes of the size 1–4 regression lines are similar for both sites.

In contrast to marrow yields, flesh yields are negatively, and, with the exception of size 3–4 animals from FLKN 1/2, significantly related to skeletal part abundance (figure 3*a*, *b*, table 2). Further, when long bone flesh yields are considered alone, there are no significant relationships within or between size classes, unlike those found for marrow yields (table 2). The results on tissue yields suggest that skeletal part representation at the two sites is related to marrow extraction and not flesh consumption, as is consistent with hominid scavenging.

These indications of scavenging, however, may be partly spurious. The low representation of post-cranial axial flesh-bearing parts might not result from their largely defleshed state and consequent neglect by hominids at the death site, but rather from their preferential destruction subsequent to defleshing by hominids. This alternative is supported by the significant, or nearly significant, positive relationships at both sites between MAU and bulk density of bones (table 2). Post-cranial axial bones have the lowest bulk density (table 1), making them less resistant to destructive agents than denser long bones and head parts.

Density-dependent skeletal part profiles have been suggested to have many potential causes (Lyman 1984). The most likely causal agent at the sites in question, however, is ravaging of hominid-butchered bone by site scavengers such as hyenas. Carnivore coprolites and tooth-marked bone are present at both sites (Bunn 1986; Leakey 1971). Also, recent experiments demonstrate a strong positive relationship between bone density and the survivorship of bones fed on by spotted hyenas (Marean & Spencer 1991). Indeed, the number of vertebrae, pelves, ribs, and hindlimb bones at the two sites under examination are significantly and positively correlated to their survivorship under the influence of spotted hyena ravaging (Marean *et al.* 1991).

The representation of long bones, however, is not density-dependent. No consistent and significant relationships are obtained between long bone MAUS from either site and their bulk density (table 2). This is due to the fact that Bunn's long bone MAUS are based not only on articular ends, but also midshaft fragments. Bunn has argued that midshafts must be used to estimate long bone abundance accurately. This assertion has been confirmed by experiments showing that hyenas selectively remove grease-filled long bone epiphyses from hammerstone-broken assemblages of long bones, but virtually ignore hammerstone-generated midshafts which have been deprived of any nutrient value (Blumenschine 1988; Binford *et al.* 1988; Marean & Spencer 1991; Marean *et al.* 1991).

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† An MAU value of 1 for humeri would be obtained if two humeri were present (even if both were from the left side), because an animal has two humeri. Likewise, the presence of 27 vertebrae would yield an MAU based on vertebrae of 1.

‡ Larger mammal size classes used here are zooarchaeological standards following Bunn *et al.* (1980). Size 1 animals are less than 50 lb. live mass (e.g. Thomson's gazelle), size 2 are 50–250 lb. (e.g. Grant's gazelle), size 3 are 250–750 lb. (e.g. wildebeest and zebra), and size four are 750–2500 lb. (e.g. buffalo). 1 lb. = 0.4536 kg.

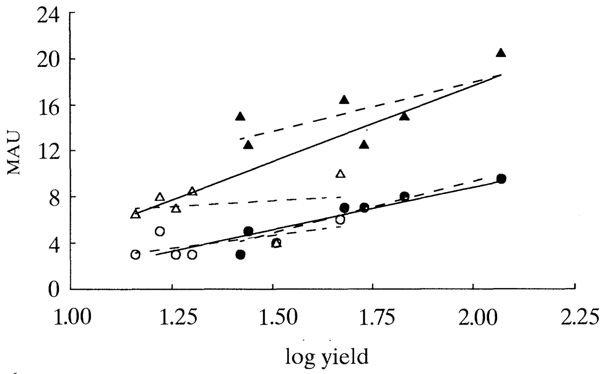

Figure 2. Marrow yields and MAU representation of long bones at FLK Zinj (circles) and FLKN 1/2 (triangles). Marrow yields (in g) are from Blumenschine & Madrigal (in preparation) and MAU values are from Bunn (1986) (see table 1). Dashed least squares regression lines are shown for size 1 and 2 bones (open symbols) and size 3 and 4 bones (closed symbols). Regression statistics (solid lines) for the combined size groups at FLK Zinj: $y = 7.3x - 5.9$, $r = 0.91$, $p = 0.0001$; and FLKN 1/2: $y = 13.2x - 8.8$, $r = 0.76$, $p = 0.004$.

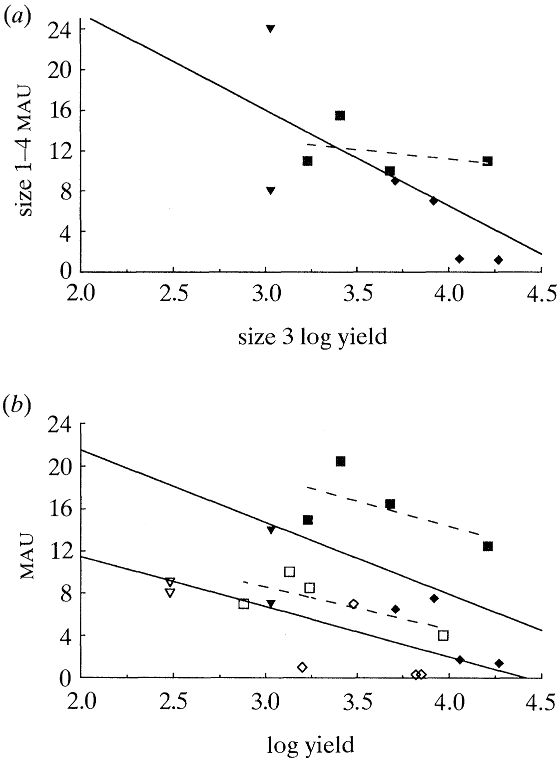

Figure 3. Flesh yields and MAU representation at FLK Zinj (*a*) and FLKN 1/2 (*b*). Flesh yields are based on Blumenschine & Caro (1986), and MAU values are from Bunn (1986) (see table 1). Open symbols, size 1 and 2 mammals; closed symbols, size 3 and 4 mammals. Diamonds, post-cranial axial bones; inverse triangles, head bones; squares, long bones. Dashed least squares regression lines are for long bones only and are based on only four points per size class as metapodials bear no flesh. Regression statistics (solid lines) are for all parts: (*a*) $y = -9.5x + 44.6$, $r = -0.67$, $p = 0.04$; (*b*) size 1 and 2 mammals, $y = -4.7x + 20.9$, $r = -0.67$, $p = 0.03$; size 3 and 4 mammals, $y = -6.8x + 35.2$, $r = -0.49$, $p = 0.15$.

4. DIET AND FORAGING

The results are consistent with hominid scavenging of mostly marrow and head contents, but are rendered equivocal owing to evidence for density-dependent destruction of some flesh-bearing parts. Ambiguity in interpretations can be reduced by focussing on long bones, which do not show density-dependent patterning, and by segregating discussion according to three component behaviours of animal food foraging by hominids. Listed in order of increasing equivocality, these are (i) marrow bone breakage, (ii) the tissue types transported from death sites, and (iii) the tissue types encountered at death sites.

Minimally, the results presented for both sites show that long bones were broken in direct proportion to their marrow yield. That hominids rather than carnivores were responsible for extracting marrow from most long bones is indicated by new data from FLK Zinj (Blumenschine & Bunn 1990) on the proportion of long bone fragments that bear percussion marks produced by hammerstone breakage (Blumenschine & Selvaggio 1988). Hence, although both assemblages contain disproportionate numbers of 'meaty' upper limb bones at the expense of 'non-meaty' metapodials (Bunn 1986; Bunn & Kroll 1986), the results show that long bone representation is conditioned by marrow (= fat) yield. Hominid breakage of marrow bones at the two sites followed an energy maximizing strategy, as might be expected if hominid populations were energy limited. Because flesh yields correlate negatively with carcass part abundance, hominids do not seem to have been protein limited.

Higher-level inferences are more equivocal. Long bones might have been transported to the sites in proportions determined by marrow yield. This would suggest that most parts were transported in a defleshed condition and that the motivation for bone transport was not flesh-sharing. Alternatively, other long bones may have been transported in proportions predicted by maximization of flesh yield, but only those which were broken for their marrow survived post-butchery ravaging because they are represented mainly by unnutritious midshaft fragments. Or, the results could indicate that flesh from many axial parts and long bones was butchered at the death site and transported without the bone, as among some hunter-gatherers today (see, for example, Bunn *et al.* (1988)).

Even more equivocal is the interpretation based on the consumption sequence analysis that hominids typically encountered most bones in a defleshed condition. This interpretation apparently contradicts Bunn's (Bunn *et al.* 1980; Bunn & Kroll 1986) inference that the presence of stone tool cut-marking on 'meaty' long bones implies hominid access to fully-fleshed or largely intact carcasses, as in early-access scavenging or hunting. However, there are no experimental or ethnographic models that permit one to equate the proportion of parts that bear cut marks with the proportion of bones that were actually defleshed or disarticulated. Further, we do not know how to distinguish cut-marking produced while defleshing whole muscle masses from that inflicted during the removal of scraps of flesh that commonly survive carnivore consumption (Blumenschine in Bunn & Kroll (1986)). Likewise, for carnivore tooth marks on bones from the two sites, we need to learn the distinction between tooth-marking associated with defleshing and that produced during bone breakage for marrow or grease extraction. An integrated analysis of the anatomical distribution of stone tool cut marks, hammerstone percussion marks, and carnivore tooth marks is needed to assess the edible tissues consumed by carnivores versus hominids, and the order in which they fed on carcasses. Such an analysis for long bones from FLK Zinj is in progress (Blumenschine & Bunn 1990). Until this independent evidence is available, however, the skeletal part data suggests that the presence at the sites of long bones that once bore meat requires neither hominid transport of long bone flesh, nor the availability of fully-fleshed bones at the death site. Skeletal part transport may instead have been based upon maximization of energy yields from marrow fat, and hominids may have typically encountered most bones already defleshed by carnivores.

5. THE SOCIO-ECONOMIC FUNCTION OF EARLY ARCHAEOLOGICAL SITES

The nutrient benefit of animal food foraging is not the only factor relevant for evaluating carcass part transport decisions made at the death site and the socio-economic function of the archaeological site to which parts were transported. These factors are defined in figure 4*a*, *b* by four sets of circumstances, including (i) predation risk, (ii) interspecific and intraspecific feeding competition, (iii) the availability of carcass processing equipment at the death site, and (iv) food yield encountered and food yield per individual in a transport party.

Carcass part transport may be constrained by energy yields and by logistical concerns (see O'Connell *et al.* (1988) for an ethnographic example). Routed foraging, involving minimal or no transport, should occur if a carcass' energy yield is too low to finance transport, if adequate processing equipment is available at the death site, and if competition and predation risk at the carcass is low (figure 4*a*). However, if transport is energetically and logistically feasible, several motivations for transport that serve to define the socio-economic function of the transport site have been specified. These can be evaluated in terms of the nutritional, logistical and ecological circumstances prevailing at the death site and transport site.

In Isaac's home base model, sharing intentions in an atmosphere of intragroup cooperation was the explicitly hypothesized motivation for the transport of surplus quantities of animal foods to archaeological sites. High carcass yields are shown in figure 4*a* to be necessary to finance transport to a central place, which, on average, will be further from the death site than the nearest refuge tree or source of stone for carcass processing. Field butchery of flesh to reduce transport costs to a central place is shown to be constained by predation risk: high risk would allow only the quick quartering of carcasses into transportable packets. A site to which carcass parts were transported can serve as a home base only if each transporter, on average, provides a surplus, and if predation risk and inter- and intraspecific feeding competition is low (figure 4*b*).

Inadequate amounts of carcass processing equipment (stone tools) at the death site are shown in figure 4*a* to promote transport to a nearby cache of usable stone created previously by hominids. Caching is not indicated in the context of low predation risk, as Potts feels that hominid involvement with carcasses would always expose them to danger and competition from carnivores. Hence, if archaeological sites were stone caches of the type envisioned by Potts, they were the setting for only hasty processing and consumption, but no other maintenance and social activities. The availability of surplus quantities of food at the cache is relevant only in terms of the amount that was wasted (figure 4*b*).

High risk of predation or interspecific competition from carnivores at the death site would promote transport to a locality where consumption can occur in relative safety (Isaac 1983). A foraging mode with this motivation can be labelled refuging. Refuging is unmotivated by equipment needs and should occur virtually regardless of available yield (figure 4*a*). If early archaeological sites were refuges they should be characterized by low levels of predation risk and competition, but, unlike central places, places to which food surpluses were not introduced intentionally (figure 4*b*). Dissemination of food among group members may occur: low available yields might render this akin to what Isaac characterized as the 'tolerated scrounging' seen during meat-eating among chimpanzees. Occasional high yields might result in '*de facto* sharing' (Isaac 1983).

Other socio-economically relevant motivations for carcass part transport may have operated. For instance, intraspecific competition at the death site might encourage individual hominids to remove carcass parts to an area where feeding could occur in isolation. Such behaviour typifies the strategy of spotted hyenas when feeding at carcasses in large groups.

Archaeologically visible criteria for measuring these constraints and motivations on carcass part transport are needed if the model in figure 4 is to serve as more than an heuristic devise for comparing competing hypotheses on hominid foraging and socio-ecology. This was the goal of the skeletal part analysis reported here with respect to carcass part yield. Although those results were equivocal in and of themselves, it should also be noted that archaeologists, including Isaac and Binford, have not been able to test whether animal foods were ever present at the sites in amounts required to sustain active sharing. They are hindered by a lack of direct evidence for (i) the number of hominids occupying these sites at any one time, (ii) the duration over which the bone assemblages accumulated (*contra* Potts 1986; see Bunn & Kroll 1987; Lyman & Fox 1989), (iii) the relative contribution of plant foods to hominid subsistence (Sept 1986), and (iv) an ignorance of whether the archaeologically visible activities of

(*a*)

		carcass yield and processing equipment needs	
		low	high
feeding competition and predation risk	low	routed (no transport)	transport to: central place (field butchery possible)
	high	transport to: refuge	transport to: refuge, cache, or central place (minimal field butchery)

(*b*)

		food yield per transporter	
		no surplus	surplus
feeding competition and predation risk	low	refuge (with tolerated scrounging?)	central place (with sharing)
	high	cache	cache (with waste)

Figure 4. (*a*) Nutritional, logistical and ecological circumstances at the death site that define the type of site to which carcasses are transported, and (*b*) circumstances at the transport site that define the socio-economic function of the site.

stone tool discard and carcass processing were typical or rare elements of hominid adaptation. None the less, if long bone marrow was the main benefit of animal food foraging, the food value introduced to the sites seems small. Based on data in table 1, the long bones at FLK Zinj and FLKN 1/2 contained a total of 3234 and 6743 grams of marrow, respectively. Assuming that (i) all marrow was composed soley of fat, (ii) there are 9 Kcal g^{-1} of fat, and (iii) that the minimum daily caloric requirement of an adult Plio-Pleistocene hominid was 2000 Kcal, then the marrow bones at FLK Zinj represent 14.6 person-days of caloric intake, and those at FLKN 1/2 represent 30.3 person-days. Assuming further that one carcass was acquired each day the sites were used by a hominid group, the minimum number of mammal carcasses at FLK Zinj (48) and FLKN 1/2 (45) indicate a daily availability of 30% and 67% of a single adult's daily caloric requirements, respectively. This energy yield may have been adequate to provision infants (Isaac 1983; C. Peters, personal communication), but rather than promoting cooperative sharing, such small amounts of easily defended, energy-dense marrow might instead encourage intragroup competition. Clearly, these estimates of animal food value at the sites should be seen as minima. Nonetheless, if animal-food sharing was anywhere as regular and economically central as it is in modern hunter-gatherers, the cut mark data will have to show that flesh was the mainstay of the system.

Archaeological detection of the degree of predation risk and competition with carnivores is also complicated. Potts (1984) argued for a high degree of competition and risk on the basis of the presence of carnivore bones at the sites, and evidence for hasty carcass processing from the presence of some complete, unbroken long bones. However, given the tree-climbing abilities of Plio-Pleistocene hominids (Susman & Stern 1982), carcass parts should have been transported to the vicinity of climable trees where ready refuge from predators could be found if necessary. Such refuging, as in savanna-woodland baboons today, should characterize hominid foraging even if they were not carnivorous. Any additional risk encountered at animal death sites could be minimized by scavenging from abandoned kills (Blumenschine 1987), as is consistent with results of the consumption sequence analysis presented here.

Evidence for the adequacy of processing equipment at the death site will require experimental studies that examine the minimum amount of stone needed to process a carcass of a particular size and completeness. If this amount is small, then such equipment may have been routinely carried by hominids on foraging expeditions. If larger, as I suspect it was for complete processing of most larger mammal carcasses, sites might represent a combination of refuges and *de facto* stone caches. That is, sites are places originally chosen for carcass processing on the basis of the refuge they offered; the same place would be revisited with locally acquired carcass foods because usable stone remaining from prior processing episodes could supplement that which was routinely carried. This site function can accommodate the interpretation of skeletal part profiles presented here, and could account for the accumulation of the bone and stone at FLKN 1/2 and FLK Zinj.

The socio-economic function of sites such as FLK Zinj and FLKN 1/2 is in these ways conditioned by opportunities and constraints on hominid diet and foraging. Their actual socio-economic function will become apparent only if we gain a better understanding of (i) the timing of carnivore and hominid involvement with carcass parts and the tissues consumed by each, (ii) the amount and types of stone tools needed to butcher a carcass of a particular size and completeness, and (iii) the ecological setting of the sites, including the proximity of refuge trees and the extent of competition between hominids and carnivores. Most of these issues are currently the subject of investigation among Early Stone Age archaeologists, the results of which will lead to a greater understanding of the nature and circumstances of hominid subsistence and social evolution.

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Discussion

A. Whiten (*Scottish Primate Research Group, University of St Andrews, U.K.*). My question is about the extent to which scavenging would have been a drastic tactic for a primate to adopt. On the occasions I have observed baboons come across a lion kill they have given it a wide berth, despite the fact that when they make their own kills the meat is highly valued and intensely competed over. In Dr Blumenschine's carcass watches, has he observed primates' reactions?

R. J. Blumenschine. My observations of over 250 fresh carcasses in the Serengeti include only one episode in which non-human primates (olive baboons and vervet monkeys) influenced the consumption of a scavengeable carcass. A large troop of baboons displaced a female leopard with her large cub from their resting tree that was adjacent to another harbouring a half-eaten Thomson's gazelle kill (Cavallo & Blumenschine 1989). The baboon troop fed for several hours on pods from the *Acacia* resting tree, never having become obviously aware of the carcass despite its close proximity. Later, John Cavallo (personal communication) observed the same troop driving the same female leopard off another tree-stored kill. This time, two adult baboons inspected the carcass briefly without feeding on it before joining the rest of the troop to feed on pods at the base of the storage tree. For all other, terrestrial carcasses I observed, baboons were simply not in the vicinity, suggesting that their range use is constrained by that of larger predators like lions and spotted hyenas.

Despite anecdotal exceptions (see, for example, Hasegawa *et al.* (1983)) scavenging by non-human primates seems rare (see Strum 1983). It has never been reported on carcasses larger than themselves. Even if they shun the drastic tactic of usurping prey from predators larger and more social than the leopard, non-human primates are simply not equipped to benefit nutritionally from vertebrate foods that come in packages too large to deflesh and disarticulate with their teeth and hands, and whose bones are too stout to be broken (for marrow and brains) manually. This constraint was not present for hominids possessing the simple slicing and pounding tools of the earliest stone industry. Hunting large mammals, given the lack of obvious projectile weaponry for the great majority of prehistory, can be argued to have been a far more difficult tactic for acquiring these, and a less parsimonious explanation for their regular presence at early archaeological sites.

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K. Hawkes (*Department of Anthropology, University of Utah, Salt Lake City, U.S.A.*). Dr Blumenschine briefly mentioned the results of his experiments with Curtis Marean on hyena carcass processing, but did not refer to them in his conclusions. Would he comment further on those results and their implications for interpreting the Oldowan?

R. J. Blumenschine. The work with Curtis Marean (Marean *et al.* 1991) shows that captive spotted hyenas preferentially remove axial parts (pelves, vertebrae and ribs), then limb ends, from assemblages of experimentally butchered bones, leaving behind an assemblage dominated by limb shafts. Preliminary analyses of similar experiments conducted with free-ranging carnivores in the Serengeti by Sal Capaldo support this result. Such selective removal of axial parts can produce skeletal part profiles that mimic those attributed to selective transport of limbs from death sites to archaeological sites by hominids, as argued by Henry Bunn (see Bunn 1986). I identified in my paper a third process that might produce the limb-dominated skeletal part profiles, namely, unselective acquisition by hominids of the only parts that remain with scavengeable food on a carcass defleshed and abandoned by felids. The equifinality can only be broken by using independent lines of evidence, which I suggest in the paper to derive from ongoing studies of the anatomical distribution and incidence of carnivore tooth marks and stone tool butchery marks on bone surfaces.

Because the relevant experiments and archaeological applications are in progress, my conclusions were explicitly equivocal. We do not know whether the bone assemblages were created at death sites, or if they represent whole-carcass transport to a processing locale followed by hyaenid scavenging, unselective transport of parts from carcasses found largely defleshed, or selective transport of limbs from more fully fleshed carcasses acquired by hunting or scavenging. What we have learned from my paper is that marrow bones were broken in direct proportion to their fat yields, a nutritional strategy for which low-risk scavenging of abandoned kills in riparian habitats is totally consistent. Clearly, our analyses and models need further refinement, and promising efforts cited above are in progress.

K. Hawkes. Dr Blumenschine did not mention the work on bone transport patterns among the Hadza presented by Bunn *et al.* (1988), and by our own group (O'Connell *et al.* 1988, 1990). Could he be invited to address the implications of this work for the interpretations of variation in body-part representation in archaeological assemblages, especially with respect to Isaac and Bunn's arguments about the evidence for large body part transport at Plio-Pleistocene sites such as Koobi Fora and Olduvai?

R. J. Blumenschine. O'Connell *et al.* (1988) have shown that the skeletal parts transported by the Hadza from kill sites to camp sites vary among and within prey taxa. Inclusion of Bunn *et al.*'s (1988) data set, argued by Bunn's team to be consistent with the premise that limb-dominated assemblages signal selective food transport by hominids to ancient 'camp' sites, does not change their conclusion: for most taxa, Hadza preferentially transport axial parts, often having processed and discarded limb bones at or near the death site. O'Connell *et al.* (1990) conclude that limb-dominated skeletal-part profiles are not a secure signature of food transport by hominids, a behaviour upon which the veracity of the food sharing or home-base model rests (Isaac 1978; Bunn 1986). This conclusion is strengthened by recent demonstrations that two processes in addition to hominid transport decisions can produce limb dominated assemblages (see my response to Professor Hawkes' first question and my paper in this symposium).

The Hadza results, however, do not as yet provide incisive criteria for interpreting skeletal part profiles with regard to prehistoric hominid transport decisions or site function. Hadza behaviour is archaeologically relevant only to the extent that the mechanisms which transform their behaviour into bony residues are understood and shown to be sufficiently fundamental as to have conditioned prehistoric residues of behaviour in the same way. O'Connell's team has made important strides in explaining variability in the proportion of a carcass' skeleton that is transported from a death site through recourse to fundamental energy optimizing mechanisms related to carcass size, size of transport parties, and distance of a kill site to a camp site. However, as O'Connell's group states, they currently lack the data (net nutrient yields of carcass parts, as these vary with carcass taxon, size and age) which are crucial for explaining variability in the particular bones – for example, axial *versus* limb – that are transported. Until these data are available, archaeologists must rely on criteria other than skeletal part profiles to assess hominid transport of carcass foods and its implications for the socio-economic function of archaeological sites.

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