Long-distance carcass transport at Olduvai Gorge? A quantitative examination of Bed I skeletal element abundances

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ABSTRACT

Relative abundances of skeletal elements at Plio-Pleistocene archaeological sites have long been interpreted to represent selective transport of portions of large prey. Models from optimal foraging theory suggest that the degree of carcass transport selectivity reflects transport constraints, particularly transport distance. A quantitative analysis of skeletal element abundances in five bone assemblages from Bed I, Olduvai Gorge, indicates that within the subset of elements most likely to resist attritional processes, there is no evidence for preferential transport of small or large mammals. The results suggest relatively low carcass transport costs and are most consistent with site formation models favoring short-distance carcass transport. The data are also consistent with the possibility that hominins were not responsible for transporting bones at some sites. Several Bed I assemblages, with the exception of FLK-*Zinjanthropus*, lack evidence of a functional relationship between flaked stone artifacts and the faunal remains, such as cut-marks or percussion-marks on bone. In conjunction with the skeletal part data, this suggests that hominin involvement with the bone assemblages was minimal at all sites but FLK-*Zinjanthropus*. The patterning at Bed I contrasts strongly with Middle Stone Age and Middle Paleolithic assemblages, which provide clear evidence for selective transport, suggesting higher transport costs and longer transport distances.

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Introduction

Ethnographic observations indicate that hunters faced with carcass transport constraints must select a limited number of body parts for transportation from the kill site to the consumption site (Yellen, 1977; Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988a, 1990; Bartram, 1993b; Abe, 2005). These observations provide underlying support behind the long-standing zooarchaeological tradition of examining the relative abundances of skeletal parts in order to interpret butchery and transport decisions (White, 1952, 1953, 1954, 1955; Perkins and Daly, 1968). The incorporation of skeletal element analysis into foraging theory models has provided faunal analysts with the tools to examine butchery and transport decisions in relation to energetic costs and returns (Broughton, 1994, 1999; Grayson and Cannon, 1999; Cannon, 2003; Marean and Cleghorn, 2003; Egeland and Byerly, 2005; Nagaoka, 2005, 2006; Faith, 2007). Examination of skeletal element abundances within the context of foraging theory stems largely from Binford's ethnoarchaeological study of the caribou-hunting Nunamiut (Binford, 1978). Binford reasoned that the nutritional value of different body parts plays a critical role in determining Nunamiut butchery and transport decisions. He collected data from caribou (*Rangifer tarandus*) and sheep (*Ovis aries*) carcasses to develop indices of the economic utility of skeletal portions as a tool for examining their frequencies in bone assemblages. Binford's development of economic utility indices assumes that people optimally forage across carcasses of large prey in the same manner that people optimally forage for prey across larger landscapes (Grayson, 1988, 1989). It is now widely accepted that butchery and transport decisions are mediated by the economic value of different body parts in relationship to the energetic costs of transporting them (Bunn et al., 1988; Metcalfe and Jones, 1988; O'Connell et al., 1988a, 1990; Bartram, 1993b; Cannon, 2003).

The analysis of skeletal element frequencies within a foraging theory framework can be used to examine the carcass transport decisions of Plio-Pleistocene hominins. Were butchery and transport decisions constrained by long-distance carcass transport, similar to that documented for modern hunter-gatherers

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(e.g., Bunn et al., 1988; O'Connell et al., 1988b, 1990; Bartram, 1993b), or by rather short-distance carcass transport, perhaps on the scale of only tens to hundreds of meters? Among carnivores, short-distance transport has been defined as that regularly documented in their peripheral transport of prey from kill sites, less than 500 meters, in contrast to longer-distance transport to their dens (Domínguez-Rodrigo, 1994). In human foragers, short-distance transport of complete carcasses has been documented among the Hadza to be between 3 and 5 km, and long-distance transport, which includes discard of carcass remains at the kill site, from 5 km to more than 14 km (Bunn et al., 1988). Answers to the question of carcass transport behavior is relevant to one of the most contentious issues in Plio-Pleistocene archaeology: What is the behavioral significance of Plio-Pleistocene archaeological sites (e.g., Domínguez-Rodrigo et al., 2007; O'Connell et al., 2002, and references cited therein)? Do they represent "central places" to which Plio-Pleistocene hominins transported fully fleshed animal carcasses from long distances (Isaac, 1978, 1983)? Or were they "near-kill accumulations" to which hominins brought small quantities of meat and marrow from carcasses defleshed and abandoned by carnivores nearby (O'Connell et al., 2002)? The goal of this study is to assess Plio-Pleistocene hominin carcass transport strategies through a quantitative examination of skeletal element abundances recovered from five sites in Bed I, Olduvai Gorge, Tanzania.

Historical background

Associations of fragmented faunal remains with flaked stone artifacts in Plio-Pleistocene archaeological sites traditionally justified the interpretations of these sites as "living floors" (Leakey, 1971), "home bases", or "central-place foraging sites" (Isaac, 1978, 1983), to which hominins transported a variety of foods, especially meat acquired from big-game hunting. This interpretation provided the basis for assigning numerous modern human behavioral characteristics to early *Homo*, including reciprocal food sharing, sexual divisions of labor, and the emergence of nuclear families (Isaac, 1978; Clark, 1997).

Binford (1981) suggested that the associations of stone tools with animal remains were coincidental at some sites, likely reflecting time-averaged palimpsest accumulations. At the same time, however, documentation of stone-tool-inflicted cut-marks on bones from Olduvai Gorge and Koobi Fora established a direct behavioral connection between the hominins, the stone artifacts, and the faunal remains at a few sites (Bunn, 1981; Potts and Shipman, 1981). Although cut-marked bone provided direct evidence for hominin meat-acquisition, the behavioral implications of these data were not settled. Binford (1981) reasoned that the cut-marks were the result of hominins scavenging small amounts of meat and marrow from carcasses already preyed upon by large carnivores. According to Binford, there was no evidence that hominins transported carcass remains long distances from the point of acquisition, that meat was shared among hominins, or that meat contributed substantially to the hominin diet.

In order to develop more strongly warranted inferences regarding the hominin contribution to these bone assemblages, paleoanthropologists directed their efforts towards studying early archaeological sites from a taphonomic perspective (e.g., Bunn and Kroll, 1986; Marean et al., 1992; Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998; Domínguez-Rodrigo et al., 2007). This research has led to a general consensus that the faunal remains recovered from most Plio-Pleistocene archaeological sites are the product of hominin behavior. These sites are generally thought to represent locations to which hominins transported carcass remains for processing and consumption (reviewed by O'Connell et al., 2002). Beyond this generalization, however, opinions are still conflicting. Following Isaac's (1978) original perspectives, some continue to view the Plio-Pleistocene archaeological sites as central place sites, to which hominins transported fully fleshed carcass remains from distant locations (e.g., Bunn and Kroll, 1986; Rogers et al., 1994; Rose and Marshall, 1996; Domínguez-Rodrigo, 1997; Bunn, 2001). Others favor what O'Connell and colleagues (2002) dubbed the "near-kill accumulation model" in which the Plio-Pleistocene sites are viewed as locations where hominins consumed small amounts of meat and primarily marrow or head contents from carcasses previously defleshed and abandoned by carnivores (e.g., Blumenschine, 1991; Selvaggio, 1994; Capaldo, 1997); substantial carcass transport from the point of acquisition is not inferred (but see Blumenschine et al., 1994). The latter interpretation has been challenged by recent taphonomic evidence (Domínguez-Rodrigo et al., 2007).

Differential skeletal element representation has figured strongly in various site formation models (Isaac, 1978; Binford, 1981; Bunn, 1986; Bunn and Kroll, 1986; Potts, 1988; Capaldo, 1997; Domínguez-Rodrigo, 2002; O'Connell et al., 2002). As noted by Bunn (1986), faunal assemblages from Plio-Pleistocene sites contain numerous meaty appendicular elements, whereas axial elements, including vertebrae, ribs, and pelves, are less abundant. Bunn (1986: 680) concluded that "selective transport of mainly appendicular parts of carcasses of large animals was the dominant process leading to the observed patterns of skeletal representation at the central place sites." This argument has been challenged on the taphonomic grounds that the observed patterns of skeletal element representation are also consistent with documented patterns of carnivore destruction (Marean et al., 1992). Since Marean and colleagues' (1992) criticism, the extent to which the skeletal element abundances support selective transport is no longer clear. New examinations that take into account taphonomic destruction are required in order to develop behavioral inferences from the skeletal part data.

The purpose of this study is to contribute to the debate surrounding the nature of Plio-Pleistocene archaeological sites through quantitative examinations of skeletal element representation. Skeletal element abundances from five assemblages excavated by Leakey (1971) from Bed I, Olduvai Gorge, are analyzed. Results are compared to three Middle Stone Age (MSA)/Middle Paleolithic (MP) assemblages where there is well-established evidence for selective carcass transport, presumably over long distances. The overall patterning of skeletal element abundances is interpreted within a foraging theory framework to provide insight into the costs that mediated butchery and transport decisions, and how they varied across assemblages.

The Bed I study sites

Leakey (1971) excavated numerous archaeological sites from Bed I, dating to ca. 1.85–1.75 Ma (Walter et al., 1991). Here we examine skeletal element abundances from five assemblages: FLK North: Levels 1/2, 3, and 4; FLK-*Zinjanthropus*; and FLK NN: Level 1 (Table 1). The skeletal element data represent the efforts of the most recent examination of the Bed I archaeofaunas, undertaken by Domínguez-Rodrigo et al. (2007).

Table 1
Summary of Bed I assemblages examined in this study (from Leakey 1971).

Site	Faunal remains	Artifacts	Manuports
FLK North: Levels 1/2	3,510	1,205	210
FLK North: Level 3	1,254	171	39
FLK North: Level 4	929	67	17
FLK-*Zinjanthropus*	3,410	2,470	96
FLK NN: Level 1	275	16	18

The first three faunal assemblages were recovered from various levels in the FLK North site. FLK North: Levels 1/2, 3, and 4 were described by Leakey (1971) as sites where faunal remains and artifacts were dispersed throughout a clay horizon. Archaeological remains from Levels 1/2 and 3 were recovered from a 2–3-ft layer of gray-brown silty clay. Level 4 is a distinctive darker-brown clay horizon, which varies in thickness from 1.5 ft to 3 in. High frequencies of carnivore coprolites and regurgitated material indicate that carnivores were active at Level 4 (Leakey, 1971). The faunal assemblage recovered from Levels 1/2 represents one of the principal sources of data, in addition to FLK-*Zinjanthropus* (below), for which selective transport of meaty appendicular elements has been inferred (Bunn, 1986).

The FLK-*Zinjanthropus* archaeofauna has been the focus of heated debates for over twenty-five years, largely owing to its expansive and well-preserved sample (Binford, 1981, 1988; Bunn and Kroll, 1986; Binford et al., 1988; Potts, 1988; Blumenschine, 1995; Capaldo, 1997; Domínguez-Rodrigo, 1997, 1999; Selvaggio, 1998; Domínguez-Rodrigo and Barba, 2006). The faunal remains provide evidence for a taphonomic history involving both carnivore and hominin agents. Much of the debate surrounding this assemblage concerns the relative contributions of these agents to the formation of the assemblage and, by extension, whether hominins enjoyed early or late access to carcass remains (i.e., the hunting vs. scavenging debate). Leakey (1971) characterized the site as a "living floor," and it is a classic representation of what would traditionally be referred to as a central place foraging site.

The final assemblage examined in this study was recovered from Level 1 of the FLK NN site. Level 1 is a clay horizon yielding a low-density scatter of fauna and stone artifacts. Following Leakey (1971), this assemblage represents yet another "living floor," which can be stratigraphically linked to FLK-*Zinjanthropus*.

Explaining carcass transport decisions

For large prey that cannot be transported intact, foragers must make decisions about which body parts to transport. In the case of large vertebrates, foragers can increase energetic return rates by processing the prey at the point of acquisition in order to maximize the proportion of high-utility elements selected for transport (e.g., White, 1954; Perkins and Daly, 1968; Binford, 1978; Thomas and Mayer, 1983). Theoretical models have been developed to examine the trade-offs between transport costs and field-processing costs (Metcalfe and Barlow, 1992; Bettinger et al., 1997; Cannon, 2003); the implications of these models with respect to transport behavior have been explored in ethnographic and archaeological case studies (O'Connell et al., 1990; Barlow and Metcalfe, 1996; Bettinger et al., 1997; Bird and Bliege Bird, 1997; Broughton, 1999; Bird et al., 2002; Cannon, 2003; Nagaoka, 2005; Faith, 2007).

From these models, it is apparent that transport distance is one of the critical factors underlying carcass transport decisions. At low transport distances, a forager can maximize return rates by spending minimal amounts of time processing the prey at the point of acquisition. As carcass transport distance increases, return rates can be maximized by increasing the amount of time spent processing the prey and selecting a more limited subset of body parts for transport. Ethnographic observations of modern hunter-gatherers support these predictions (Bunn et al., 1988; O'Connell et al., 1988a, 1990).

Carcass transport behavior is also known to be influenced by additional constraints, including transport mode, the number of carriers, the number and size of carcasses transported, geographic features, and even the time of day and season of prey acquisition (Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988a, 1990; Bartram, 1993a,b; Abe, 2005). Despite the many variables known to

influence transport behavior, we favor the interpretation of the skeletal part data in terms of transport distance because (1) foraging theory makes explicit predictions as to how distance will influence transport behavior (e.g., Cannon, 2003) and (2) distance has consistently been shown to influence carcass transport decisions in ethnographic (O'Connell et al., 1988a, 1990) and archaeological (Broughton, 1999, 2002; Cannon, 2003; Nagaoka, 2005; Faith, 2007) case studies.

The application of foraging theory models to the Bed I archaeofaunas allows for interpretation of skeletal element abundances in terms of the costs mediating butchery and transport decisions, particularly transport distance. Differences in the degree of transport selectivity across the five Bed I sites and the later MSA/MP sites highlight probable differences in transport constraints and site functions.

Methods

Examination of skeletal element abundances was accomplished here through the integration of a taphonomic model of bone survivorship with a novel approach for quantifying skeletal element frequencies (Faith, 2007; Faith and Gordon, 2007). Details are provided below.

A taphonomic model of bone survivorship

A range of destructive taphonomic processes, particularly carnivore gnawing, are known to alter skeletal element frequencies following human discard (Lyman, 1994, and references therein). Thus, interpreting skeletal element abundances in terms of carcass transport behavior requires that faunal analysts consider only those elements that accurately reflect their original abundances. On the basis of actualistic, ethnoarchaeological, and archaeological data, Marean, Cleghorn, and colleagues have shown that skeletal elements can be divided into high- and low-survival sets (Marean and Frey, 1997; Marean and Cleghorn, 2003; Cleghorn and Marean, 2004, 2007). The high-survival set is characterized by elements with thick cortical walls lacking cancellous bone and includes long-bone midshafts and portions of the cranium and mandible. In contrast, the low-survival set includes elements with thin cortical walls and low-density, grease-rich cancellous portions, such as vertebrae, ribs, pelves, scapulae, and long-bone epiphyses. Phalanges and small, compact bones are also considered low-survival elements since they are readily consumed by carnivores (Marean, 1991). High-survival elements represent the best candidates for analyzing skeletal element abundances and interpreting carcass transport decisions. In contrast, the frequencies of low-survival elements are highly sensitive to destructive processes that have acted on an assemblage following human discard; they should not be considered as directly indicative of human behavioral patterns in assemblages subjected to destructive processes.

This distinction between high- and low-survival elements is based largely on models of carnivore bone-destruction. Carnivores have been observed to affect faunal assemblages in a broad range of geographic and environmental contexts (Sutcliffe, 1970; Binford, 1981; Haynes, 1982; Binford et al., 1988; Marean and Spencer, 1991; Marean et al., 1992; Blumenschine and Marean, 1993; Faith and Behrensmeyer, 2006). Numerous archaeological bone assemblages also bear evidence of carnivore destruction in the form of tooth-marks on bone (Monahan, 1996; Marean and Kim, 1998; Marean et al., 2000; Domínguez-Rodrigo et al., 2002; Assefa, 2006). The Bed I archaeofaunas are no exception and carnivores have been implicated in the taphonomic histories of several sites, including FLK-*Zinjanthropus* and FLK N: Levels 1/2 (Leakey, 1971; Potts, 1988; Marean et al., 1992; Blumenschine and Marean, 1993;

Domínguez-Rodrigo et al., 2007). The following analysis includes only those elements in the high-survival set: the cranium, mandible, femur, tibia, metatarsal, humerus, radius, and metacarpal.

Because destructive taphonomic processes do not permit analysis of the entire vertebrate skeleton, the degree of transport selectivity can only be examined within the high-survival subset. Although far from ideal, such is the reality of studying carcass transport behavior in assemblages subjected to attrition, as in the Bed I sites (Bunn, 1986; Blumenschine and Marean, 1993; Domínguez-Rodrigo et al., 2007). Fortunately, the high-survival subset includes elements of varied economic utility values (Metcalfe and Jones, 1988), meaning that it should be possible to detect differential transport of high- versus low-utility elements (Faith and Gordon, 2007). In addition, Faith and Gordon (2007) showed that subtle variations in carcass transport selectivity within the high-survival subset can be detected through a quantitative approach.

Quantifying skeletal element abundances

Faith and Gordon (2007) demonstrated that skeletal element abundances can be quantified using an evenness index (see also Faith, 2007). They noted that the degree of selectivity in which foragers transport carcasses will be reflected in the evenness of the distribution of specimens across classes of elements (Fig. 1). In situations where entire carcasses are transported, or where no transport has occurred at all, there should be a perfectly even distribution of skeletal elements (standardized by their frequency in the vertebrate body). As transport becomes more selective and favored elements are increasingly overrepresented, the evenness of the frequency distribution of skeletal elements will decline.

Following Faith and Gordon (2007), skeletal element evenness was measured using the Shannon evenness index, where evenness $= -\Sigma p_i \ln p_i / \ln S$, and S is the number of elements (e.g., humerus, femur) and p_i is the standardized proportion of specimens of the ith element. A maximally even distribution of skeletal elements takes an evenness of 1.000, with values approaching zero as evenness declines. In measuring skeletal element evenness, it is necessary that bone frequencies be standardized by their actual frequencies in the vertebrate body. Frequencies were standardized using minimal animal units (MAU) after Binford (1984).

Skeletal element evenness was calculated for both small (size classes 1–2, after Brain, 1981) and large mammals (size classes 3–4) in each of the five Bed I assemblages. As emphasized by Faith and Gordon (2007), skeletal element frequencies from excavated assemblages should be considered samples from a larger population of skeletal elements. Sampling error can introduce substantial deviations from the underlying population of skeletal elements, especially at small sample sizes. To understand how observed evenness values reflect the underlying population values, 95% confidence limits for the evenness index were generated by bootstrapping the skeletal element frequencies 10,000 times. Bootstrap confidence limits were obtained using the bias-adjusted
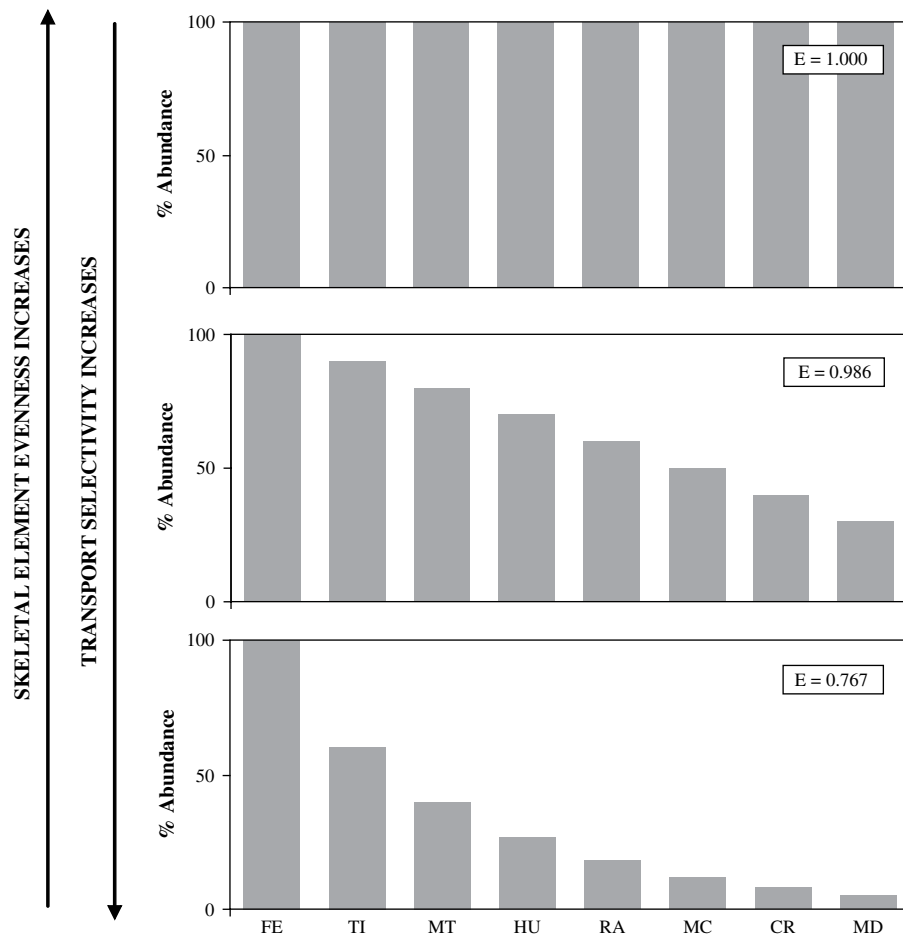

Figure 1. The relationship between carcass transport selectivity and skeletal element evenness for three hypothetical assemblages. The upper assemblage displays a perfectly even distribution with all high-survival skeletal elements equally represented. As carcass transport becomes increasingly selective in the middle and bottom assemblages, evenness declines. FE = femur, TI = tibia, MT = metatarsal, HU = humerus, RA = radius, MC = metacarpal, CR = cranium, MD = mandible.

standard bootstrap method (Manly, 1997). Confidence limits that exclude values of 1.000 provide statistically significant evidence for an uneven distribution of skeletal elements within the high-survival subset (i.e., selective transport). In contrast, confidence limits that include 1.000 cannot be distinguished from a population characterized by a perfectly even distribution of skeletal elements. We note that an analysis of the eight high-survival elements as opposed to the two or three dozen elements traditionally examined limits the statistical power of our analysis. As discussed above, however, this is necessary in order to circumvent the problem of density-mediated attrition when inferring carcass transport behaviors.

A note on estimating skeletal element abundances

We use MAU to interpret carcass transport behavior. The MAU counts are based on the minimum number of elements (MNE) standardized by their frequency in the vertebrate skeleton. Accurate estimates of long-bone abundance require that shaft fragments be considered (Bunn and Kroll, 1986; Marean and Spencer, 1991; Marean and Frey, 1997; Marean and Kim, 1998; Pickering et al., 2003; Marean et al., 2004), and this was done for the Bed I assemblages. The protocol for estimating long-bone abundances follows the procedure described by Bunn and Kroll (1986) for the FLK-*Zinjanthropus* assemblage. All specimens (i.e., shafts and epiphyses) for a given element and size class were laid out and systematically examined in order to determine the minimum number of elements that could account for all specimens on the basis of overlapping portions, refits, size/morphological differences, etc. Long-bone MNE counts are reported for anatomically complete elements rather for proximal or distal ends. The MNE counts for crania and mandibles included complete tooth rows and isolated teeth in the calculations. The petrosal was also included in MNE determinations for crania (for further details, see Domínguez-Rodrigo et al., 2007).

Results

High-survival skeletal element abundances for small and large mammals are provided in Table 2. All analyses of the Bed I assemblages are based on the values reported in this table.

Prior to inferring how skeletal element abundances reflect human behavioral patterns, it is necessary to demonstrate that their abundances have not been altered by density-mediated attrition (Lyman, 1984, 1985, 1993, 1994; Grayson, 1989). Here we examine whether or not the high-survival subset of elements displays evidence of such attrition. Since most of the mammal remains from Bed I are bovids (Leakey, 1971), maximum shape-adjusted bone density values for wildebeest (*Connochaetes taurinus*) are used here (Lam et al., 1999). Intertaxonomic variation in

bone density values is minimal (Lam et al., 1999). For all assemblages, skeletal element abundances are not significantly correlated with bone density (Table 3). Thus, density-mediated attrition does not explain the observed frequencies of high-survival skeletal elements.

Skeletal element evenness values and their 95% confidence limits are provided in Table 4 and illustrated in Figs. 2 and 3. In each Bed I assemblage, skeletal element evenness values are high and the confidence limits always include 1.000. The inclusion of 1.000 within the confidence limits indicates that we cannot reject the null hypothesis that skeletal elements were sampled from a perfectly even distribution. Within the high-survival subset of elements, there is no clear evidence for selective transport in any of the Bed I assemblages. These patterns are consistent across our small (size 1–2) and large (size 3–4) body size divisions.

The lack of evidence for selective transport within the high-survival subset at Bed I is emphasized by a comparison to more recent MSA/MP cave assemblages (Table 5). Comparisons include the small and large ungulates from MSA Layers 10 and 11 at Die Kelders Cave in South Africa (Marean et al., 2000), the small and large mammals recovered from MSA deposits at Porc-Epic Cave (Assefa, 2006) in Ethiopia, and the small (size 2 only) ungulates from MP deposits at Kobeh Cave (Marean and Kim, 1998). For these assemblages, skeletal element evenness values and their 95% confidence limits are provided in Table 6 and displayed graphically in Figs. 2 and 3. For the small mammals, there is clear evidence for selective transport at Porc-Epic Cave and Kobeh Cave. Only for the Die Kelders Cave small ungulates do the 95% confidence limits of skeletal element evenness include 1.000. With respect to the large mammals, skeletal element representation at Die Kelders Cave and Porc-Epic Cave is consistently uneven, providing evidence for selective transport within the high-survival subset.

Discussion

The analysis of Bed I skeletal element abundances reveals that the frequencies of crania, mandibles, and long-bone elements cannot be distinguished from a perfectly even distribution of elements. Thus, there is no evidence for selective transport within the high-survival subset in any of the five Bed I assemblages. These patterns contrast strongly with skeletal element frequencies at later MSA/MP assemblages, which show clear evidence for preferential transport within this subset of elements.

Assuming that carcasses were transported, it is possible to reconcile the skeletal part data with two hypothetical carcass transport strategies:

(1) *Transport of complete or near-complete carcasses.* The even distribution of high-survival elements could result from the transport of complete or near-complete carcasses, i.e., an

Table 2
High-survival skeletal element abundances (MAU) for small and large mammals across the five Bed I study sites.

Element	FLK N: Levels 1/2		FLK N: Level 3		FLK N: Level 4		FLK-*Zinj*		FLK NN: Level 1	
	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large
Cranium	13	29	5	6	3	7	3	7	N/A	6
Mandible	13	29	7	8	3	8	7	14	N/A	8
Femur	5.5	19	5	4	2.5	2	4	7	N/A	1.5
Tibia	11.5	31	6.5	8.5	1.5	3.5	6	9.5	N/A	1
Metatarsal	10	24	3.5	4.5	1.5	7.5	5	3	N/A	1.5
Humerus	11.5	21.5	6.5	7.5	4	3	3	7	N/A	2
Radius	9.5	18	6	7.5	3	3.5	3	8	N/A	1.5
Metacarpal	9	14.5	7	4	1	6.5	3	5	N/A	2
Σ	83	186	46.5	50	19.5	41	34	60.5	0	23.5

Table 3
Rank-order correlation between bone density (Lam et al. 1999) and skeletal element abundances (MAU) for large and small mammals across the Bed I assemblages.

Site	Correlation	
	r_s	p
FLK N: Levels 1/2		
Small mammals	−0.157	0.711
Large mammals	0.024	0.955
FLK N: Level 3		
Small mammals	−0.413	0.310
Large mammals	−0.663	0.073
FLK N: Level 4		
Small mammals	−0.381	0.352
Large mammals	−0.060	0.888
FLK-Zinj		
Small mammals	−0.203	0.630
Large mammals	−0.561	0.148
FLK NN: Level 1		
Small mammals	–	–
Large mammals	0.061	0.885

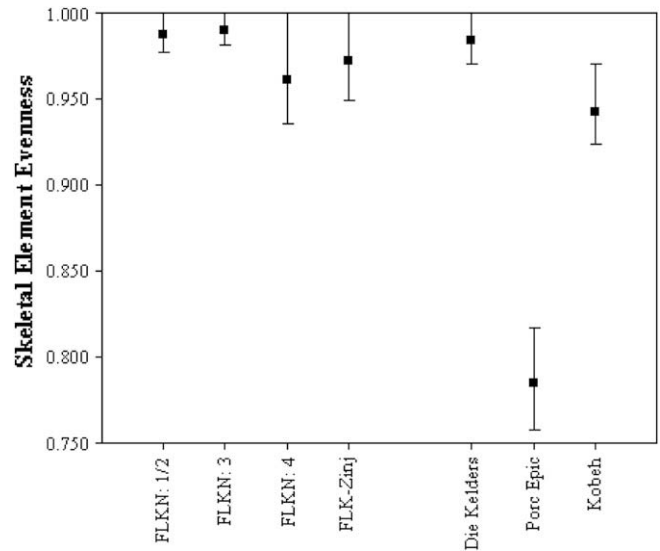**Figure 2.** Small-mammal skeletal element evenness and 95% confidence limits for the Bed I and MSA/MP assemblages. See also Tables 4 and 6.

unconstrained transport strategy (Faith and Gordon, 2007). Such a transport strategy is characterized by no preferential selection of particular elements. Low frequencies of axial remains (Bunn, 1986) are explained by postdiscard destructive processes, including carnivore consumption (Marean et al., 1992).

(2) *Unselective transport of crania and long-bones with rare transport of other elements.* This transport strategy represents the most selective scenario that is compatible with the skeletal element data. Such a model of carcass transport has been proposed by Blumenschine (1991) in the context of a scavenging scenario. However, this carcass transport strategy is equally applicable to an early access scenario. Low frequencies of axial elements are explained as a function of differential transport (Bunn, 1986, 2007).

In the absence of techniques for accurately estimating the numbers of low-survival elements that were originally deposited at these sites, the two transport strategies are indistinguishable from each other on the basis of high-survival skeletal element abundances. Regardless of which interpretation is favored, however, both scenarios share one commonality: the lack of evidence for selective transport of high-survival elements suggests that transport costs never reached the point where energetic returns could be increased by culling these elements at the point of prey acquisition. Thus, transport costs were relatively low.

The skeletal element abundance data from the MP/MSA assemblages provide an interesting contrast. At these sites, the skeletal element evenness values, with one exception, provide clear evidence for selective transport. The exception is the small mammal assemblage from Die Kelders Cave, many specimens of which are size 1 ungulates (62% of the total MAU), which may not necessitate substantial amounts of field processing prior to transport. Marean and colleagues (2000) provided evidence that a large component of the size 1 ungulate assemblage was accumulated by raptors rather than humans; selective transport is not expected in this situation. In general, it can be inferred that transport costs in the MP/MSA assemblages were high enough to require selective transport within the high-survival subset of elements. Transport costs were apparently higher in these assemblages than at Bed I. The obvious question, then, is: Why the difference in transport costs?
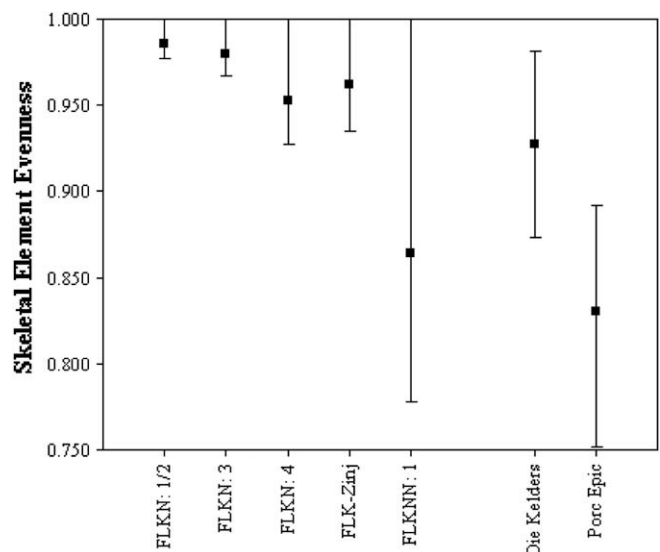
Table 4
Skeletal element evenness and 95% confidence limits for the Bed I assemblages.

Site	Evenness	
	Observed	95% confidence limits
FLK N: Levels 1/2		
Small mammals	0.987	0.977–1.000
Large mammals	0.986	0.977–1.000
FLK N: Level 3		
Small mammals	0.990	0.981–1.000
Large mammals	0.980	0.967–1.000
FLK N: Level 4		
Small mammals	0.961	0.936–1.000
Large mammals	0.953	0.927–1.000
FLK-Zinj		
Small mammals	0.972	0.949–1.000
Large mammals	0.962	0.935–1.000
FLK NN: Level 1		
Small mammals	–	–
Large mammals	0.864	0.778–1.000

Figure 3. Large-mammal skeletal element evenness and 95% confidence limits for the Bed I and MSA/MP assemblages. See also Tables 4 and 6.

Table 5
High-survival skeletal element abundances (MAU) across three Middle Stone Age and Middle Paleolithic assemblages.[a]

Element	Die Kelders Cave		Porc-Epic Cave		Kobeh Cave
	Small	Large	Small	Large	Size 2
Cranium	7	3	5	0.5	9.5
Mandible	5	0.5	10	1.5	11
Femur	7	5	158	17.5	31.5
Tibia	7	8	49	8	48
Metatarsal	4.5	7	22.5	9	18
Humerus	5	7.5	29.5	6	32
Radius	3	5	77	5	24
Metacarpal	5	3	17.5	1.5	19
Σ	43.5	39	368.5	49	193

[a] Die Kelders Cave layers 10 and 11 small and large ungulates (Marean et al., 2000); Porc-Epic small and large mammals (Assefa, 2006); and Kobeh Cave size 2 bovids/cervids (Marean and Kim, 1998).

One of the key points to be taken from foraging theory models is that a forager should spend more time processing prey at the location of prey acquisition as transport distance increases (O'Connell et al., 1988a, 1990; Metcalfe and Barlow, 1992; Barlow and Metcalfe, 1996; Bettinger et al., 1997; Bird and Bliege Bird, 1997; Broughton, 1999; Bird et al., 2002; Cannon, 2003; Faith, 2007). The greater transport costs evident in the MP/MSA assemblages could be explained by long-distance prey acquisition. Longer-distance prey acquisition implies elevated search times and transport distances, resulting in increases to overall costs (e.g., Cannon, 2003). Conversely, the relatively low transport costs incurred in transporting carcasses to the various Bed I sites can be explained by relatively short-distance transport.

We can only speak of transport costs, and by extension transport distances, in relative terms. If anything is to be taken from ethnographic observations of hunter-gatherer carcass transport behavior, it is that transport decisions are mediated by numerous situational constraints, including transport distances, but also transport mode, the number of carriers, the number and size of animals transported, geographic features, and even the time of day and season of prey acquisition (Binford, 1978; Bunn et al. 1988; O'Connell et al. 1988a, 1990; Bartram 1993a,b). Thus, interpreting skeletal element abundances and transport selectivity in terms of actual transport distances (i.e., interval scale) is not warranted. We are, however, more confident in our ability to compare *relative* transport costs (i.e., ordinal scale) between the Bed I assemblages and the MP/MSA assemblages. On the basis of skeletal element representation, it is apparent that transport costs incurred during the formation of the Bed I archaeofaunas were lower than those in the MP/MSA assemblages. A broad range of theoretical, ethnographic, and archaeological research gives us good reason to believe that transport distance is a driving factor behind the differences in transport costs (O'Connell et al., 1988a, 1990; Metcalfe and Barlow,

Table 6
Skeletal element evenness and 95% confidence limits for three MSA/MP faunal assemblages.

Site	Evenness	
	Observed	95% confidence limits
Die Kelders Layers 10/11		
Small ungulates	0.984	0.970–1.000
Large ungulates	0.927	0.873–0.981
Porc-Epic Cave		
Small ungulates	0.785	0.758–0.817
Large ungulates	0.830	0.752–0.892
Kobeh Cave		
Size 2 bovid/cervid	0.942	0.924–0.970

1992; Barlow and Metcalfe, 1996; Bettinger et al., 1997; Bird and Bliege Bird, 1997; Broughton, 1999; Bird et al., 2002; Cannon, 2003; Nagaoka, 2005; Faith, 2007). In the following discussion we use the terms "long-distance transport" and "short-distance transport": we stress that these reflect ordinal-scale differences in transport distance.

If the Bed I assemblages are the product of an unconstrained transport strategy, in which complete carcasses were transported across the landscape, transport distances were likely low. Long-distance transport of complete small carcasses may be feasible, but becomes increasingly unlikely as prey size increases to include size 3 (84–296 kg) and 4 (>296 kg) mammals, which almost certainly require substantial amounts of field butchery prior to long-distance transport. It is highly unlikely that complete large-mammal carcasses were hauled long distances across the Plio-Pleistocene landscape. Ethnographic evidence provides unequivocal support for this argument (Yellen 1977; Binford 1978; Bunn et al. 1988; O'Connell et al. 1988a, 1990; Bartram 1993b; Monahan 1998; Abe 2005).

If the Bed I assemblages are the product of unselective transport of crania, mandibles, and long-bones to the general exclusion of other elements, long-distance transport remains unlikely. As transport distances increase, at some point the efficiency-minded forager is going to stop transporting low-utility elements (e.g., metapodials, crania, mandibles; see Metcalfe and Jones, 1988) and become increasingly selective—even within the high-survival set of elements. This transport threshold appears to have been reached on a regular basis in the later MSA/MP assemblages we examined. The MSA/MP foragers routinely abandoned low-utility elements in favor of body parts providing higher energetic returns (Marean and Kim, 1998; Marean et al., 2000; Assefa, 2006; Faith and Gordon, 2007).

An alternative hypothesis

Thus far, we have discussed Bed I carcass transport strategies under the explicit assumption that faunal remains were transported in the first place. An alternative hypothesis that is equally consistent with the skeletal part data is that carcasses were not substantially transported by any agent, and following Binford's (1981) critique, the association between flaked stone artifacts and the faunal remains is entirely fortuitous. For example, according to Isaac's (1981, 1983) "common amenity hypothesis," certain places on the landscape, such as a shade tree or water hole, could have attracted both hominins and carnivores on a regular basis. Repeated visits to such locations, perhaps never at the same time, could result in associations of flaked stone artifacts and the prey of large carnivores. The hypothesis that the spatial association between the artifacts and the faunal remains is coincidental can be rejected at FLK-*Zinjanthropus*, where abundant cut-marks and percussion-marks provide direct evidence for hominin involvement with the bone assemblages (Potts and Shipman, 1981; Bunn and Kroll, 1986; Blumenschine, 1995; Domínguez-Rodrigo, 1997, 2002). However, high frequencies of hominin-modified bone have not been reported for any of the additional assemblages. A recent analysis shows that, with the exception of FLK-*Zinjanthropus*, there is minimal evidence for these hominin behavioral traces in the Bed I sites (Domínguez-Rodrigo et al., 2007). In light of the skeletal part data and the lack of hominin behavioral traces on the bones, a reconsideration of the hominin contribution to the bone assemblages at FLK North: Levels 1/2, 3, 4 and FLK NN: Level 1 is necessary.

Leakey (1971) noted that the fauna and archaeological remains from FLK North: Levels 1/2, 3, and 4 were dispersed throughout the thickness of two clay horizons. These sites lack the apparent spatial integrity of the "living floors" such as FLK-*Zinjanthropus*, and could

very well record a palimpsest of behavioral traces over long periods of time. Perhaps due to some local geographic feature (e.g., a water hole or spring), the FLK North site acted as a magnet on the paleolandscape, repeatedly attracting hominins, large herbivores, and their predators. Estimates of the amount of time-averaging involved in the accumulation of early Pleistocene sites range from the scale of several decades (Kroll, 1994) to over a century (Blumenschine and Masao, 1991) and perhaps a millennium (Stern, 1993). Such estimates certainly allow for sufficient time-averaging to generate large, archaeologically visible, indirect associations between flaked stone artifacts and faunal remains.

In contrast to the FLK North site, FLK NN: Level 1 was described by Leakey (1971) as a "living floor," which is stratigraphically correlated to the FLK-Zinjanthropus "living floor." However, evidence for hominin activity is minimal; there are only 16 artifacts from this site (Table 1). In the absence of evidence for selective transport and a functional relationship between flaked stone artifacts and the bones (i.e., cut-marks or percussion-marks), the only clear hominin contribution to the formation of this site may be the result of a minute or two of flint-knapping transposed on a relatively small bone assemblage (Tables 1 and 2).

With the exception of FLK-Zinjanthropus, variable frequencies of flaked stone artifacts provide the only unambiguous evidence for hominin activity at the Bed I sites examined in this study. In the absence of direct evidence for carcass transport or carcass processing (Domínguez-Rodrigo et al., 2007), the hominin contribution to the formation of the bone assemblages from FLK North: Levels 1/2, 3, 4 and FLK NN: Level 1 is questionable at best; non-hominin accumulation mechanisms should be reconsidered.

What about FLK-Zinjanthropus?

Following a conspicuous historical trend, the oft-debated FLK-Zinjanthropus assemblage once again stands out as a key site from which we must base our interpretations of Plio-Pleistocene hominin behavior (Bunn and Kroll, 1986; Binford, 1988; Binford et al., 1988; Blumenschine, 1991, 1995; Oliver, 1994; Capaldo, 1997; Domínguez-Rodrigo, 1997; Selvaggio, 1998; Domínguez-Rodrigo and Barba, 2006). The evidence presented in this study suggests that FLK-Zinjanthropus was presumably a locality to which hominins regularly deposited carcass remains acquired from nearby. This, in turn, suggests that the site was in close proximity to ambush sites or similar localities where either hominins or carnivores had routine access to prey. FLK-Zinjanthropus probably represented a convenient location on the paleolandscape for hominins to transport and process prey for consumption and food sharing (Isaac, 1978)—see recent taphonomic evidence for this interpretation in Domínguez-Rodrigo et al. (2007)—or perhaps to escape intense competition with other carnivores at the kill sites (Potts, 1984, 1988; Blumenschine, 1991; Blumenschine et al., 1994; Oliver, 1994). In either case, it appears that Plio-Pleistocene hominins at FLK-Zinjanthropus transported carcasses over a more limited distance than MSA and MP hominins from Die Kelders, Porc-Epic, and Kobeh Cave. Whether the transport behavior at these three sites is representative of most late Middle Pleistocene/Late Pleistocene archaeological sites remains to be demonstrated (see Yravedra and Domínguez-Rodrigo, 2009).

Conclusions

Within the subset of skeletal elements most likely to resist attritional processes, there is no evidence for selective transport of small and large mammal carcasses at any of the five Bed I assemblages examined. At FLK-Zinjanthropus, where there is an established functional relationship between flaked stone artifacts and the faunal remains, these results suggest that carcass remains were transported over relatively short distances. This suggests FLK-Zinjanthropus and perhaps the other sites were in close proximity to ambush sites where hominins and carnivores routinely acquired prey. These results also raise the possibility that assemblages from FLK North: Levels 1/2, 3, 4 and FLK NN: Level 1 are not the product of hominin behavior (Domínguez-Rodrigo et al., 2007). Patterning of Bed I skeletal element abundances contrasts strongly with three MSA/MP assemblages, which provide clear evidence for selective long-distance transport of small and large prey.

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