

Mobility, Competition, and Plio-Pleistocene Hominid Foraging Groups

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Evidence for carcass access times and levels of early hominid mobility is synthesized using studies of carnivore ethology and theories of interspecific competition to arrive at tentative conclusions about the organization of Plio-Pleistocene hominid foraging groups. The model presented suggests that group foraging tactics, in combination with high mobility, are central to successful confrontational scavenging (interference competition), whereas individual foraging tactics and high mobility are central to successful nonconfrontational scavenging (exploitative competition). In contrast, group or individual foraging tactics and low mobility characterize the acquisition of fresh carcasses in low-competition contexts. Individual foraging tactics and low mobility are employed in response to extreme competition over marginal resources. Preliminary tests with data from Bed I Olduvai Gorge and Koobi Fora suggest that Plio-Pleistocene hominids, like other large-bodied predators, employed flexible foraging tactics involving changes in group size and levels of mobility to gain access to carcasses in both low- and high-competition contexts.

KEY WORDS: Plio-Pleistocene; early hominid behavior; carnivore behavior; interspecific competition; mobility; archaeology; Bed I Olduvai Gorge; Koobi Fora.

INTRODUCTION

This paper is concerned with detecting variability in early hominid tactical mobility through the application of a set of different analytical procedures to the much-studied Plio-Pleistocene archaeological assemblages from Bed I Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. Tactical mobility, or the movement of individuals or groups in response to situational

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variability in resource quality and availability, may have determined in part the nature of hominid access to faunal resources. Indeed, tactical mobility, in addition to flexible foraging group organization and the availability of simple processing technologies such as stone hammers and sharp stone flakes, may have played a critical role in hominid invasion of the predatory guild (see Rose and Marshall, 1996; Shipman and Walker, 1989).

The tactical mobility of Plio-Pleistocene hominids may have been substantially different from that of their immediate primate ancestors. Comparisons between modern predators and nonhuman primates suggest that hominid tactical mobility may have undergone a substantial reorganization associated with an increased emphasis on faunal resources in the diet. On the whole, predator levels of mobility far exceed those of nonhuman primates. Mean territory sizes for brown (308 km^2) and spotted (1095 km^2) hyaenas, for example, are more than an order of magnitude larger than those of chimpanzees (15 km^2) (see Nishida and Hiraiwa-Hasegawa, 1987; Mills, 1990; Wrangham *et al.*, 1993). Mean distances moved per activity period also are much greater for brown (31.1 km) and spotted (27.1 km) hyaenas compared with chimpanzees (3.9 km). The nature and distribution of faunal resources, in combination with specialized locomotory adaptations (Lewis, 1997; Van Valkenberg 1985), are primarily responsible for the high levels of mobility observed among modern large-bodied predators (e.g., Hoffer and East, 1993; see also Cashdan, 1992). In general, predators must move frequently and travel great distances to capture dispersed faunal resources. Plio-Pleistocene hominids, like other large-bodied predators, may have developed high levels of tactical mobility in response to similar resource pressures.

In addition to the problems of locating faunal resources at dispersed locations on the landscape, hominids presumably had to deal with intense competitive pressures from both conspecifics and other predatory species when foraging for faunal resources (Binford, 1981, 1984, 1985; Blumenschine, 1986a,b; Blumenschine *et al.*, 1994; Bunn and Ezzo, 1993; Potts, 1988; Rose and Marshall, 1996). In this regard, ethological studies of modern carnivores indicate that group size and the speed at which faunal resources can be located on the landscape are important determinants not only of the types of competition that will be encountered at a given faunal resource package, but also the success that individuals or groups will have in defending or pilfering those resources and the overall nutritional return (e.g., Creel and Creel, 1995; Hoffer and East, 1993; Mills, 1990; see also Rose and Marshall, 1996). Thus, the social organization of mobility, as well as the distances traveled and the speed of movement, probably played an important role in Plio-Pleistocene hominid competitive efficiency.

In this paper I use several approaches to modeling foraging mobility and a range of ecological rules of interspecific competition to generate socioecological hypotheses about the contexts in which early hominid behavioral organization may have favored individuals or groups. I evaluate these expectations against examples of faunal exploitation and lithic technological organization at several Plio-Pleistocene (ca. 1.9–1.5 Mya) archaeological sites. The sites included in this study are FLK “Zinjanthropus,” FLK North 6, FLKN 1–2, FLKNN-2, FLKNN-3, and DK from Olduvai Bed I and FxJj 50 from Koobi Fora (Bunn, 1982, 1986; Bunn *et al.*, 1980; Leakey, 1971; Potts, 1988; Toth, 1982). Many of the conclusions of this study are complementary to those reached by other researchers and suggest interesting relationships between earlier models of Plio-Pleistocene hominid behavior.

MOBILITY AND COMPETITION

Questions of adaptive mobility have become a topic of central concern in anthropology and archaeology in recent years (e.g., Binford, 1978, 1979, 1980; Cashdan, 1992; Kelly, 1983, 1992, 1995; Kuhn, 1992, 1994, 1995; Mandryk, 1993; Shott, 1986, 1996). In general, mobility is seen as a means of “averaging over” variability in the spatial and temporal distribution of resources (Cashdan, 1992, p. 237; Kelly, 1983, 1992). The concept of mobility includes several dimensions: (1) individual mobility, or the movement of individuals independent of one another; (2) group mobility, or the coordinated movement of individuals; and (3) the frequency and magnitude of movement (see Kelly, 1983, 1992, p. 44). These dimensions of mobility are often tightly interrelated on the ground, but for conceptual reasons it is important to view them as having separate organizational implications. For example, group mobility involves not only organizing principles associated with individual movement, but also a different order of planning that takes into consideration the abilities and needs of individual foragers and the mechanisms for organizing cooperation. Moreover, individual mobility, group mobility, and the frequency and magnitude of mobility provide different options for dealing with specific foraging dilemmas; certain foraging tasks may be best accomplished by individuals, while others require group action. For historical, theoretical, and methodological reasons, archaeologists have concentrated primarily on the relationship between the frequency and magnitude of mobility and the organization of technology (Kelly, 1992; Kuhn, 1995; Nelson, 1991). All three dimensions, however, are expected to be important in confronting the array of technological and logistical problems arising from the exploitation of spatially and/or temporally displaced resources.

The methodological and theoretical frameworks established for the study of hunter-gatherer mobility have considerable potential for expanding our understanding of early hominid behavioral organization (e.g., Kuhn, 1995; Lieberman and Shea, 1994; Stiner and Kuhn, 1992). Yet it must also be recognized that mobility models derived from modern ethnographic contexts may not be directly applicable in "premodern" contexts without certain modifications (see Freeman, 1968; Tooby and DeVore, 1987). The modifications to these models suggested in this paper are based on ecological principles of interspecific competition and follow from the observations that Plio-Pleistocene hominids were incorporating substantial quantities of faunal resources in their diet and that hominid strategies for the exploitation of faunal resources overlapped significantly with those of contemporaneous carnivores (Binford, 1981, 1985; Blumenschine *et al.*, 1994; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; Marean *et al.*, 1992; Potts, 1983, 1988, 1991; Potts and Shipman, 1981; Rose and Marshall, 1996; Stiner, 1991a,b, 1992, 1994). Plant resources also likely played an important role in organizing hominid mobility (see Bunn and Ezzo, 1993; Sept, 1992, 1994). However, resource competition probably was not as salient in this regard. I argue, therefore, that interspecific competitive interactions during the course of foraging for faunal resources were the prime driving forces behind the organization of Plio-Pleistocene hominid mobility.

Competitive interactions between early hominids and other large carnivores could have taken a variety of different forms (Binford, 1981, 1984, 1985; Blumenschine *et al.*, 1994; Bunn and Ezzo, 1993; Potts, 1988, 1991; Rose and Marshall, 1996). Interspecific competition may arise where two or more species exploit the same resources, and where the modes of resource exploitation by individuals or groups of one species reduce access to, or the quality of, resources available to others (Schoener, 1983, p. 257; see also MacArthur and Levins, 1967). In general, interspecific competition can take the form either of active interference or of passive exploitation (Begon *et al.*, 1990, p. 244; Krebs and Davies, 1993, pp. 102–118; Schoener, 1983). Active interference often involves direct confrontation between individuals, whereas passive exploitation is principally nonconfrontational. Interference competition involves reducing access to resources through active defense or pilfering of particular resource packages. Spotted hyenas and lions in the Serengeti, for example, frequently pilfer carcasses from one another (Hoffer and East, 1993; Kruuk, 1972; Mills, 1989, 1990). Contemporary hunter-gatherers such as the Hadza also have been observed actively pilfering carcasses from large carnivores (Bunn *et al.*, 1988; O'Connell *et al.*, 1988). In both the human and the carnivore examples, successful defense or pilfering of a carcass via confrontation appears to depend upon the speed with which prey or carcasses can be located on the landscape.

and the size of the foraging group. In essence, larger foraging groups, whose mobility patterns also enable them to locate prey or carcasses earlier in their resource lives, tend to be more successful in defending or pilfering large resource packages.

In contrast, exploitative competition frequently involves individual exploitation of smaller, poorer quality (i.e., marginal) resource packages (Schoener, 1983, pp. 257–258). Conceptually, as ecological space becomes more densely packed, high quality resources are consumed by the more efficient foragers (Krebs and Davies, 1993, pp. 102–105). Under such exploitative pressure, less efficient foragers are forced to subsist on more marginal resources. Such competitive forcing need not involve direct confrontation. Rather, exploitative competition *indirectly* reduces access to, or the quality of, certain resources available to other animals. Research on the foraging behaviors of brown hyaenas suggests, moreover, that the success of exploitative competition hinges on the mobility of the individual animal (Mills, 1989, 1990); individuals appear to have an advantage in quickly locating and consuming small or marginal resource packages such as ostrich eggs, small prey (e.g., birds, rodents, reptiles), or previously ravaged carcasses, largely because they have greater flexibility in their patterns of movement and tend not to attract other competitors. The tendency to organize around small group or individual foraging tactics under high exploitative pressure has been observed for a range of nonhuman primates and carnivores (Wrangham *et al.*, 1993).

The above discussion suggests that mobility and sociality (group and individual organization) are related to the types of interspecific competition that may be encountered during resource exploitation, as well as the overall success of foraging. It is not surprising, therefore, that Shipman and Walker (1989) identify mobility and sociality as two central behavioral features in the evolution of the carnivora. Although hominids are comparative “late-comers” to the carnivore guild (Stiner, 1994, p.16), it is likely that varied mobility and social tactics also played important roles in early hominid competitive interactions with the larger carnivores.²

The notion of adaptive mobility I develop here focuses on relatively short-duration and short-distance tactics used in locating and consuming limited resources under intermittent competitive pressures. Short-duration

²It is important to recognize that the role assigned to competition in this paper is meant to apply primarily to aspects of early hominid behavioral organization. Considerable controversy surrounds evolutionary models of competition-driven character displacement [i.e., “the ghost of competition past” (Arthur, 1987; Connell, 1980; Vrba, 1992)]. This controversy has resulted in a more general skepticism about the validity of interspecific competition as an ecological concept [e.g., Roughgarden (1983) and Simberloff (1983)]. Yet I believe that the difficulties in identifying the effects of past competition in the evolution of morphological traits are separate from identifying the role of competition in organizing behavior.

mobility tactics may be implemented over time periods lasting from only a few minutes to perhaps several days. Short-distance mobility tactics may be implemented over foraging paths ranging from only a few hundred meters up to a few kilometers. Both tactics are most likely implemented when foragers are confronted with "time-stressed activities" (Torrence, 1983, 1989). Time-stress refers to situations (e.g., competitive interactions) where the time available for resource capture and processing is more of a limiting factor in deciding how to organize foraging activities than the expected energy return from that resource (Torrence, 1983, p. 12). Thus, *tactical* mobility refers to behaviors different from, though not incompatible with, the large-scale "foraging" and "collecting" *strategies* thought to describe contemporary and more recent prehistoric hunter-gatherers [Binford, 1980; Lieberman and Shea, 1994]; see Krebs and Davies (1993, pp. 244-245) for a discussion of the differences between tactics and strategies in evolutionary ecology].

INTERSPECIFIC COMPETITION AND TIMING OF CARCASS ACCESS

The nature and intensity of interspecific competition between foraging predators are often dependent on the condition of carcasses when they are encountered. In the Serengeti, carcasses generally persist on the landscape for very short periods of time (Blumenshine, 1986a,b; Blumenshine and Cavallo, 1992). In other circumstances, carcasses may persist on the landscape for much longer periods of time (Capaldo and Peters, 1995; Haynes, 1982; Lyman, 1989, p. 162). Competition for a carcass early in its resource life often is a dangerous undertaking, sometimes involving direct confrontation between competing individuals. Later in the resource life of a carcass individuals may be able to avoid direct interactions with other predators, circumventing any immediate danger. The tradeoff is that predators falling at the end of a long feeding succession are forced to subsist on resources greatly reduced in quantity and quality. Thus, the time when a given predator arrives at a carcass is critical to determining not only the potential nutritional reward, but also the nature and intensity of interspecific competition encountered.

Figure 1 provides an analytical framework for assessing the timing of carcass access in terms of the disarticulation and consumption of a medium-sized bovid (72-320 kg) (Blumenshine, 1986a; Blumenshine and Cavallo, 1992, p. 93; Lyman, 1994, pp. 147-149). The sequence provides a means of characterizing the types of competitive interactions encountered at a carcass in various stages of dissarticulation and dispersion. The se-

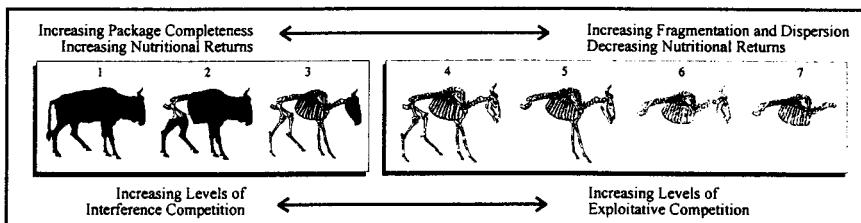


Fig. 1. The sequence of consumption and disarticulation of a carcass is divided into seven stages of increasing fragmentation and dispersion and decreasing nutritional returns. The types of competition encountered at a carcass are partially dependent upon the timing of carcass access. After Blumenshine and Cavallo (1992).

Table I. Ranked Consumption Sequence for Medium Bovids^a

Stages 1–3		Stages 4–6	
Carcass unit	Rank	Carcass unit	Rank
Hindquarter flesh		Hindlimb marrow	
Pelvis	1	Femur	13
Lumbar	3	Tibia	14
Femur	2	Metatarsal	16
Tibia	7	Phalanges	15
Forequarter flesh		Forelimb marrow	
Ribcage	4	Humerus	17
Scapula	6	Radius	19
Humerus	5	Metacarpals	20
Radius-ulna	9	Phalanges	18
Cervical	8		
Head flesh		Head contents	
Tongue	10	Maxilla pulp	21
Mandible	11	Mandible pulp	23
Maxilla	12	Brain	22
		Frontal pulp	24

^aAfter Lyman (1994, p. 149). See also Blumenshine (1986a).

quence is divided into seven stages of decreasing nutrient returns and decreasing package completeness. In general, when both flesh-eating and bone-crushing carnivores have access to a carcass, the hindquarter flesh is consumed prior to the forequarter and head flesh (Table I; Fig. 1, Stages 1–3). Similarly, hindlimb marrow is consumed prior to forelimb marrow and head contents (Table I; Fig. 1, Stages 4–6). This consumption sequence

is determined primarily by the anatomy and nutritional status of the predator and prey animals, the time available for consumption, and the number of competing predators that visit the carcass (Blumenschine, 1986a; see also Haynes, 1982; Hill, 1979; Lyman, 1994, pp. 144–150).

Whereas Blumenschine's (1986a) consumption sequence reflects what occurs at a carcass in high competition contexts, Potts (1983; see also Hill, 1979) suggests that natural disarticulation sequences more accurately represent the sequence of elements available for transport away from a carcass. While the potential behavioral and taphonomic differences between these two models are significant, one should recognize that the archaeological correlates for consumption and natural disarticulation sequences are very similar. The only major difference between the two models is in the order of forelimb and hindlimb disarticulation: Blumenschine's (1986a) consumption sequence has removal of the hindlimb elements prior to forelimb elements. Thus, at one level, the ratio of forelimbs to hindlimbs in an assemblage could serve as a measure of the timing of carcass access (Potts, 1983). On the basis of the consumption sequence model, for example, higher frequencies of forelimbs in a bone assemblage would tend to suggest slightly later carcass access. However, when the disarticulation sequence model is applied to the same assemblage, slightly earlier carcass access is indicated. I suggest that both models may be appropriate, albeit in different contexts. Where carcasses persist on the landscape for extended periods of time in low competition contexts, natural disarticulation sequences may indeed be more appropriate for describing the elements available for transport at different stages in the resource life of the carcass. Where there is a rapid and intensive succession of carnivores at a carcass, however, the consumption sequence model may be more appropriate.

At one level, the sequence of carnivore consumers at a carcass may change continuously as a result of their differing nutritional statuses (e.g., hunger) and processing morphologies (e.g., tooth and jaw architecture). As a consequence, the types of competition encountered at a carcass may change with the sequence of carnivores. A distinction can be made between the types of competition encountered in consumption Stages 1–3 and Stages 4–7 (Fig. 1). In general, only bone-crushing predators (e.g., hyaenas) and tool using hominids have full access at Stages 4–7, whereas a full range of flesh-eating (e.g., lions, leopards), bone-crushing and tool-using predators have access at Stages 1–3 (Blumenschine and Cavallo, 1992). The range of potential competitors is narrower in Stages 4–6 than in Stages 1–3.

At another level, the taphonomic changes associated with the decomposition, disarticulation, and dispersion of a carcass tend to push competitive interactions from situations of interference competition, early in the resource life of the carcass (Stages 1–3), to situations of exploitative com-

petition, late in the resource life of the carcass (Stages 4–7). In the most basic terms, a complete carcass is nutritionally more “attractive” in that it offers a greater quantity and higher quality of resources than dispersed and semiskeletonized fragments. For this reason, competitors may be more willing to risk interference at complete carcasses. However, even where competitors encounter one another at a fresh carcass, they still may avoid direct conflict (Mills, 1990, pp. 59–65), relying if possible on intimidation rather than force. At the other end of the continuum, highly fragmented and dispersed carcasses are less “attractive” to potential competitors. Individual foragers, however, still may exploit the lesser quantity and lower quality of resources present at dispersed carcasses for a substantial (if lower) nutritional return. *Hyaena* gnawing and ingestion of fragmentary skeletal elements at den sites, food caches, or other dispersed locations on the landscape, for example, represent low-risk exploitative resource use (see Lam, 1992; Mills, 1990; Sutcliffe, 1970). Given these two extremes, it may be suggested that the position of a carnivore in the behavioral succession at a carcass (from complete to dispersed) will determine whether a particular competitive framework involved active interference, passive exploitation, or some intermediate combination of the two. And, of course, feeding successions may be long and complex or short, depending upon factors such as community structure and population densities. For example, feeding successions in a community with only two large predator species and low predator-prey population densities may be substantially different from those in a community with five predator species and high predator-prey population densities (see Lewis, 1997; Van Valkenberg, 1985, 1988, 1996).

Studies of modern carnivores suggest, however, that we should be careful not to assume that specific carnivores *always* have access to carcasses at the same stage of disarticulation (Kruuk, 1972; Mills, 1990; Schaller, 1972). The timing of carcass access for certain predators can vary substantially across the environment that they inhabit. While some carnivores appear to be “obligate hunters” (e.g., wolf), and others “obligate scavengers” (e.g., brown *hyaena*), others employ extremely flexible tactics in carcass exploitation (Stiner, 1991b, 1994, pp. 250–270). Thus, it is possible for the same carnivore to occupy various positions in the feeding succession at a carcass. The spotted *hyaena*, for instance, is both a formidable social predator and a successful interference competitor (early carcass access) but will also frequently ingest dispersed bone chips (very late carcass access) (Kruuk, 1972; Mills, 1990; Sutcliffe, 1970). Given these observations, it would be inappropriate to assume that early hominids regularly occupied only one successional position at a carcass (*contra* Binford, 1981, 1984, 1985). Rather, models concerning modern carnivores lead us to expect that

the timing of carcass access may have been highly variable for hominids, depending upon such contingencies as the local environmental context of exploitation and the equipment immediately available for carcass processing. As a consequence, we might expect that early hominids engaged in a range of competitive interactions at carcasses with varying results.

INTEGRATING MOBILITY AND COMPETITION VARIABLES

The ethological observations presented above concerning predator foraging tactics and competitive interactions encountered at a carcass provide a general framework for characterizing possible hominid foraging tactics under similar competitive pressures. In particular, the above observations stress that tactical mobility, group size, and timing of carcass access are essential elements of effective interspecific competition. Numerous archaeological signatures have been suggested for identifying and characterizing the timing of carcass access (e.g., Blumenschine, 1995; Oliver, 1994; Potts, 1983, 1988; Potts and Shipman, 1981; Stiner, 1994) and tactical mobility (e.g., Binford, 1979, 1980; Kelly, 1992; Kuhn, 1991, 1995; Lieberman and Shea, 1994; Stiner and Kuhn, 1992). Here I present a model integrating archaeological measures of the timing of carcass access and levels of tactical mobility as a means of inferring general aspects of early hominid foraging group size.

Figure 2 divides the timing of carcass access into two broad categories corresponding to early and late stages of consumption and disarticulation (Stages 1–3 and 4–7 in Fig. 1, respectively). This division conforms to the general switch from the availability of exterior soft tissues such as hind-quarter and head flesh to encased tissues such as marrow and head contents (Blumenschine, 1986a; Blumenschine and Cavallo, 1992). Similarly, mobility is divided into two broad categories corresponding to high and low levels. While the use of only two categories of mobility places arbitrary limits on behaviors that are undoubtedly continuous in nature, this distinction provides a necessary simplifying step for identifying different analytical possibilities.

The model generates four outcomes. First, high levels of mobility and early carcass access suggest a competitive framework involving high levels of interference competition (Fig. 2, Cell C). Moreover, studies of modern carnivores such as the spotted hyaena suggest that when mobility is organized around the group, the chance of successful interference competition increases (Hoffer and East, 1993; Kruuk, 1972; Mills, 1989, 1990). Thus,

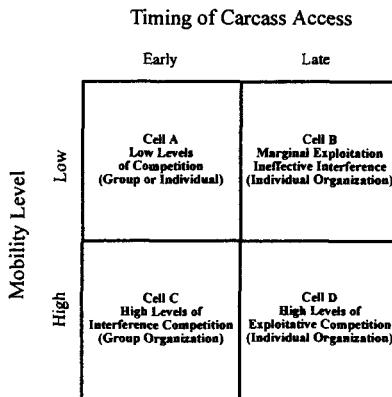


Fig. 2. The relationship between the timing of carcass access and levels of mobility may highlight specific competitive tactics employed by early hominids. Early carcass access and high levels of mobility may indicate group organization for effective interference competition (Cell C). Late carcass access and high levels of mobility may indicate individual organization for effective exploitative competition (Cell D). Early carcass access and low levels of mobility may indicate "competition-free" contexts (Cell A). Late carcass access and low levels of mobility may indicate a marginal scavenging strategy resulting from ineffective interference competition (Cell B).

in the competitive framework defined by high levels of mobility and early carcass access, early hominids may have tended to move in groups.

Second, in contexts of high mobility and late carcass access, high levels of exploitative competition instead are expected (Fig. 2, Cell D). For example, ethological studies of the brown hyaena indicate that late carcass access, when coupled with high levels of mobility, is an extremely effective strategy for individual foragers (Mills, 1989, 1990). The organization of this type of mobility around the individual forager is associated with broad areal search patterns and, thereby, provides greater returns from small or poor quality resources distributed widely over the landscape (Wrangham *et al.*, 1993; Stiner, 1991b, 1994). At the same time, the movement of individual foragers attracts less attention from other potential competitors seeking the

same marginal resources. Thus, in the competitive framework defined by high levels of mobility and late carcass access, early hominids may have tended to move as individuals.

Third, low levels of interspecific competition are indicated where low mobility is coupled with early carcass access (Cell A). In these contexts competition with other large predators probably did not drive carcass search patterns, and early carcass access presumably did not depend on tactical mobility. Such low-competition frameworks could arise through a surfeit of carcasses on the landscape such as during seasonal or catastrophic mortality gluts (e.g., Capaldo and Peters, 1995; Lyman, 1989). Alternatively, regular, exclusive access to fresh carcasses in restricted locations may have provided early hominids with low-competition contexts for resource exploitation. Blumenschine (1986b) suggests, for example, that tree-cached leopard kills in riparian woodlands are generally not accessible to other large felids and hyaenids, and could have provided early hominids with a "low-risk," predictable resource base. In either case, competition is not expected to have constrained group (or individual) mobility.

Fourth, the situation of low mobility and late carcass access implies marginal exploitation of carcasses (Cell B). Such conditions may prevail where hominid foraging strategies are ineffective in the face of intense interference competition. This scavenging niche may be so marginal, opportunistic, or unpredictable that only individual mobility may have been feasible (e.g., Binford, 1984). Such situations could arise, for example, if carcass exploitation potentially involved direct confrontation during all stages of disarticulation. In these circumstances, carcass acquisition would have been a risky strategy at all times. These conditions may indicate that alternative resources such as local flora were the focus of foraging activities (e.g., Sept, 1992, 1994). The absence of evidence for Plio-Pleistocene plant use, however, precludes archaeological tests about how such resources may have influenced the organization of individual or group mobility.

The critical point to recognize about integrating measures of the timing of carcass access and levels of tactical mobility is that, taken together, they are far more informative about early hominid behavioral ecology than either one alone. Early carcass access, for example, does not demonstrate that early hominids were effective interference competitors. Complete carcasses also could have been procured occasionally in low competition contexts and therefore tell us little about whether early hominids were efficient interference competitors. High-competition contexts and effective interference competition might be indicated, however, if early carcass access were paired with high levels of foraging mobility. Thus, the addition of evidence for variable levels of early hominid mobility may clarify whether the timing of carcass access was (or was not) competitively stressed on a regular basis.

At the same time, mobility alone says little about early hominid competitive efficiency. Archaeological evidence for how mobility influenced the exploitation of specific resources (e.g., meat and marrow) is required to elucidate the nature and efficiency of early hominid competitive interactions.

A PLIO-PLEISTOCENE CASE STUDY

Plio-Pleistocene archaeological sites in Bed I Olduvai Gorge, Tanzania, provide a basis to begin exploring the model outlined above. Although the data are less than ideal in places, there are some advantages in focusing on such a well studied area, including (1) an extensive understanding of the sedimentology and chronology of the region (Hay, 1976; Walter *et al.*, 1991); (2) detailed studies of the lithics and fauna from a variety of theoretical and methodological perspectives, including attention to taphonomy and formation processes (Leakey, 1971; Bunn, 1986; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; Oliver, 1994; Petraglia and Potts, 1994; Potts, 1984, 1988, 1991; Potts and Shipman, 1981; Shipman, 1986); and (3) continued efforts to refine paleoenvironmental reconstructions of the basin through both space and time (Hay, 1976; Peters and Blumenschine, 1995; Plumer and Bishop, 1994; Sikes, 1994).

The Bed I sites considered in the following analysis are, from oldest to youngest, DK, FLKNN-3, FLKNN-2, FLK "Zinjanthropus," FLK North 6, and FLKN 1-2. All of the Bed I sites are dated on the basis of overlying and underlying volcanic tuffs to between 1.9 and 1.7 Mya (Walter *et al.*, 1991). DK is located below Tuff IB and, therefore, dates somewhat older than 1.8 Mya. FLKNN-2, FLKNN-3, and FLK "Zinj" are located above Tuff IB and below IC and date between 1.8 and 1.76 Mya. FLK "Zinj" occurs stratigraphically above FLKNN-3 and is thus younger than FLKNN-3. Finally, FLK North 6 and FLKN 1-2 occur between Tuff IE and Tuff IF, indicating that these sites date between 1.75 and 1.749 Mya. FLKN 1-2 is stratigraphically above FLK North 6 and is the youngest of the Bed I sites.

Paleoenvironmental reconstructions of the ancient Olduvai basin place the Bed I sites in a lake margin habitat, with varying degrees of open, intermediate, and closed vegetation (Hay, 1976; Peters and Blumenschine, 1995; Plumer and Bishop, 1994; Sikes, 1994). The sites at the FLK and FLK North localities may have been within 1–2 km of the lake shore (Hay, 1976; Potts, 1988). With the exception of DK, all Bed I sites formed in low-energy environments, and the deposits appear to be minimally disturbed (Hay, 1976; Petraglia and Potts, 1994; Potts, 1988). DK preserves evidence of low- to moderate-energy water flow. However, in comparison with the degree of reworking evidenced at sites in Beds II and III (Petraglia

and Potts, 1994; Leakey and Roe 1994), and at other Plio-Pleistocene localities in East Africa, the disturbance at DK appears minimal. Some degree of postdepositional bone attrition is suspected at the Bed I sites, but it has been difficult to establish the extent of this bias (Blumenschine and Marean, 1993; Marean *et al.*, 1992; Potts, 1988). Again, in comparison with other localities in Beds II and III at Olduvai and elsewhere in East Africa, the quality of bone preservation in Bed I is generally good. Importantly, bone-accumulating carnivores have had some role in the formation of the Bed I sites (Blumenschine and Marean, 1993; Marean *et al.*, 1992). FLKNN-2, in particular, is attributed to Plio-Pleistocene hyaenids (Potts, 1988). Detailed research on bone modification and other lines of zooarchaeological evidence support the conclusion that Plio-Pleistocene hominids were the primary agents of bone accumulation at the remaining Bed I sites (Blumenschine, 1995; Oliver, 1994; Potts, 1988).

Several assemblages from Plio-Pleistocene sites at Koobi Fora, Kenya, also are included in the following analyses. Excavated between the early 1970s and the 1980s, the Koobi Fora assemblages sample a broader time range than the Bed I sites (~1.9–1.5 Mya) (Bunn, 1982; Bunn *et al.*, 1980; Toth, 1982). Five Koobi Fora sites are examined in all, including FxJj 1, 3, 10, 50, and 63. Of these, only FxJj 50 has a faunal assemblage comparable in size and quality of bone preservation to the Olduvai sites. The Koobi Fora sites all provide lithic assemblages for comparison with Olduvai. FxJj 1 and 3 occur in channel contexts but do not appear to be heavily disturbed (Toth, 1982, pp. 23–24). The remaining sites, FxJj 10, 50, and 63, formed in floodplain contexts. FxJj 50 displays low levels of postdepositional disturbance. FxJj 10 and 63 display low to moderate levels of postdepositional disturbance. All Koobi Fora sites were in some way associated with braided stream channels flowing in to ancient Lake Omo. In contrast to Olduvai, the Koobi Fora sites appear to have been at least 15–20 km from the lake margin (Bunn, 1994, pp. 250–251). Table II summarizes general comparative data for the Olduvai and Koobi Fora sites.

It is important to clarify at the outset some of the problems associated with a comparative study of this nature. One potential problem arises from the use of published data derived from independent sources. Clearly, different researchers working at Olduvai and Koobi Fora have used different methodologies and have chosen to publish different aspects of their data. As a result, it is often difficult to establish the absolute comparability of these data. Two such problems with the available zooarchaeological data are of concern in the following analyses. Skeletal element data for DK, FLKNN-3, FLKNN-2, FLK North 6, and FLK “Zinj” are taken primarily from Potts (1988). Skeletal element data for FxJj 50 and FLKN 1–2 are taken from Bunn (1982, 1986) and Bunn *et al.* (1980). Differences in the

Table II. Comparative Taphonomic and Archaeological Data for the Olduvai Bed I and Koobi Fora Sites Considered in this Study^a

Site	Age Mya ^a	Mammalian Artifacts (n)	Depositional context	Water action	Bone attrition ^{a,b}	Carnivore activity ^{a,b}	References
Olduvai							
DK	>1.8	1350	1163	Lake margin-alluvial fan	Low	Low (?)	Present Leakey, 1971; Potts, 1982, 1988, 1991
FLKNN-2	1.8–1.76	324	0	Lake margin	None	Low (?)	Dominant Leakey, 1971; Potts, 1982, 1988, 1991
FLKNN-3	1.8–1.76	390	72	Lake margin	None	Low (?)	Present Leakey, 1971; Potts, 1982, 1988, 1991
“Zinj”	1.8–1.76	614	2647	Lake margin	None	Low (?)	Present Leakey, 1971; Potts, 1982, 1988, 1991
FLK North 6	1.75–1.749	740	130	Lake margin	None	Low (?)	Present Leakey, 1971; Potts, 1982, 1988, 1991
FLKN 1–2	1.75–1.749	1720	842	Lake margin	None	·	Leakey, 1971; Bunn, 1986
Koobi Fora							
Fxj 1	~1.9	·	124	Channel	Low	·	Bunn, 1982; Toth, 1982
Fxj 3	~1.9	·	117	Channel	Low	·	Bunn, 1982; Toth, 1982
Fxj 10	~1.9	·	311	Floodplain	Moderate	·	Toth, 1982
Fxj 50	~1.5	728	1436	Floodplain	Low	Present Bunn, 1982; Bunn <i>et al.</i> , 1980; Toth, 1982	
Fxj 63	1.3–0.7(?)	·	754	Floodplain	Moderate	(?)	Toth, 1982

^aUncertainties in the data indicated by (?).^bUnavailable data indicated by ·.

tabulated ungulate size classes used by these researchers are one concern; whereas Potts (1988) reports skeletal element counts for medium (Size 3) bovids, Bunn (1982, 1986) and Bunn *et al.* (1980) report counts for medium and large (Size 3 and 4) bovids combined. Some of the following assemblage comparisons are thus confounded by possible body-size effects (e.g., Lyman 1994, pp. 191, 224). A second concern involves differences in methods used for determining minimum number of elements (MNE) for bovid long bones; Potts (1988) used only articular ends for estimating limb MNE, whereas Bunn (1982, 1986) and Bunn *et al.* (1980) also used limb shaft fragments in their estimates (see Lyman, 1994, pp. 102–104). Absolute frequencies of bovid limb elements may be somewhat deflated for the sites analyzed by Potts (1988) compared with those analyzed by Bunn (1982, 1986) and Bunn *et al.* (1980). Unfortunately, it is impossible to rectify these differences from the published literature.

Another source of potential error arises from comparing assemblages of different sizes and formation histories. Statistical uncertainty tends to increase as sample size decreases, and such statistical concerns are apparent in some of the following analyses. Variations in sample size and quality may also be related to different formation histories of the various sites. Where possible, I have attempted to minimize taphonomic and formation process biases by selecting only those sites showing low levels of disturbance and postdepositional alteration.

Despite the potential sources of error mentioned above, the following comparative analyses still have heuristic value. Though difficult to establish in any absolute sense, differences in assemblage sizes and contents may in fact reflect variability in the behaviors that generated them, and it is this range of variability that is of interest here.

Timing of Carcass Access

Questions about the timing of carcass access have received considerable attention in analyses of the Olduvai faunal assemblages (e.g., Blumenschine, 1995; Bunn and Ezzo, 1993; Oliver, 1994; Potts, 1983, 1988; Potts and Shipman, 1981). Timing of carcass access has featured both in debates over early hominid hunting and scavenging (e.g., Binford, 1981; Bunn and Kroll, 1986; Potts, 1987) and as a component of specific taphonomic studies (e.g., Blumenschine and Marean, 1993; Marean *et al.*, 1992; Selvaggio, 1994). Here I assess the relative timing of carcass access using a zooarchaeological measure that tracks variation in predator hunting and scavenging strategies (Stiner, 1991a, b, 1994, pp. 259–260). Developed by Stiner (1994, pp. 250–270), this measure involves relating anatomical content

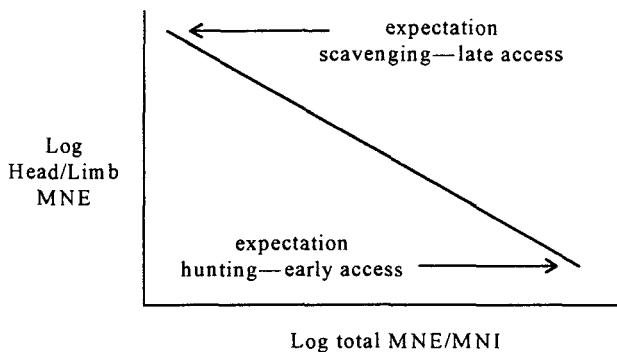


Fig. 3. The log-log relationship between anatomical content (head/limb MNE) and anatomical completeness (total MNE/MNI) appears to track hunting and scavenging strategies and potentially early and late carcass access times. Based on Stiner (1994, p. 261, Fig. 9.17).

(head/limb MNE) to anatomical completeness (total MNE/MNI) of transported faunas.³ Stiner's (1994) studies of Middle and Upper Paleolithic caves and rock shelters in west central Italy, and interspecific comparisons of modern carnivore foraging tactics, reveal a consistent pattern of an increasing ratio of head to limb elements as body part completeness in the assemblages decreases. Transported faunal assemblages dominated by head elements and incomplete carcasses appear to characterize scavenging strategies, usually of a nonconfrontational nature. In contrast, assemblages with more complete carcasses and a greater relative proportion of limb elements tend to characterize hunting or confrontational scavenging strategies (Fig. 3). Both outcomes represent broad averages of predator responses and therefore offer only general predictions about the foraging behaviors represented at individual sites.

Stiner (1994, p. 266) emphasizes both nutritional reasons for "choosing" head element transport and the effect that timing of carcass access may have on the opportunity to transport head elements (see also Binford, 1984; Speth and Spielmann, 1983). Here I focus on the latter aspects of Stiner's model and relate them to the disarticulation sequence in Fig. 1.

³MNE refers to the minimum number of complete skeletal elements necessary to account for all of the identified whole and fragmented bones in an assemblage. Head MNE is the sum of estimated complete horn cores, crania, and mandibles. Limb MNE is the sum of estimated complete appendicular elements above the feet (Stiner, 1994, p. 242). Total MNE (tMNE) is the sum of all estimated complete skeletal elements, including the axial and feet elements. MNI refers to the minimum number of individual animals necessary to account for all of the identified whole and fragmented bones in an assemblage.

In general, head elements are usually near the last to be disarticulated and consumed by modern carnivores (Fig. 1, Stage 6–7; Table I) (Blumenschine, 1986a,b; Blumenschine and Cavallo, 1992; Lyman, 1994). As a consequence, head elements are also likely to be among the last to be transported away from a death site. Early hominids encountering a carcass in the wake of a series of other carnivores may have primarily had head elements to choose from. In such a case, the range of skeletal elements available for transport would have been very narrow. In contrast, limb elements tend to be consumed, disarticulated, and possibly removed from the acquisition site earlier in the sequence (Fig. 1, Stages 4–5; Table I). Accordingly, transport of limb elements is generally dependent upon arriving at a carcass earlier in the consumption sequence. If early hominids were able to access a carcass prior to most (or all) other carnivores, they would have had a much broader range of skeletal elements to choose from; not only would head elements be available for transport, but also the marrow-rich limb elements.

From these points are derived two general archaeological expectations. First, *transported* faunas showing a clear dominance of head elements may indicate consistently later carcass access (Fig. 3). Second, a more equal representation of head and limb elements, as well as a more complete body part representation overall, may signal consistently earlier carcass access.

Stiner's approach depends upon knowing that the faunas being studied were transported. Indeed, this approach does not apply to death- or access-site assemblages. Stiner's (1994) cave and rock shelter assemblages clearly represent transported faunas. Because the Olduvai and Koobi Fora assemblages accumulated at open-air sites, we cannot be as confident that the resulting skeletal element profiles exclusively represent resource transport behaviors. While some researchers consider the Bed I sites to be death-site assemblages (e.g., Binford, 1981), Potts (1988, p. 38) has assembled a convincing case against this conclusion.

First, under conditions of normal animal turnover (attritional mortality) a very low degree of bone concentration results on the landscape. Second, relatively little mixing of the bones from the different animals occurs at death sites or over the landscapes, even where predators and scavengers have dispersed bones away from carcasses. Third, the taxonomic and ecological diversity of animals represented around death sites tends to be low. Fourth, vertebrae and other axial skeletal parts tend to remain near the death site, whereas limb bones tend to be removed. Finally, in an event or period of catastrophic mortality, such as results from a drought or flood, there may be large concentrations of carcasses, but these events leave diagnostic geological evidence.

At the same time, it is clear that a number of these zooarchaeological signatures also may arise from pre- and postdepositional processes unrelated

to hominid behavior. Blumenschine and Marean (1993) and Marean *et al.* (1992), for example, present experimental data suggesting that assemblages lacking vertebrae and ribs (i.e., "limb heavy") can result from carnivore ravaging, not just hominid transport behavior. Postdepositional bone attrition through chemical and physical agents also can lead to skeletal element profiles similar to transported assemblages (Lyman, 1994, pp. 258–263). In both cases, archaeologists are confronted with equifinality, and there appears to be no straightforward solution for untangling the overlapping signatures (see Lyman, 1994; pp. 263–281). At several Olduvai and Koobi Fora sites there are indications that both carnivore ravaging and postdepositional attrition have effected skeletal element profiles (Lyman, 1994; Marean *et al.*, 1992; Potts, 1988). For these reasons, caution is needed when one draws conclusions about hominid behavior on the basis of these bone assemblages. However, I expect that carnivore ravaging and postdepositional attrition do not invalidate Potts' (1988) general conclusion—arrived at by the remaining criteria—that the Olduvai and Koobi Fora bone assemblages represent transport behavior. Indeed, the level of bone concentration, degree of mixing, and taxonomic and ecological diversity seen in the assemblages weigh in favor of hominid transport (see also Behrensmeyer, 1993; Behrensmeyer and Boaz, 1980). I should also emphasize that the Olduvai and Koobi Fora faunal assemblages need not represent long-distance resource transport strategies characteristic of modern foragers; selective transport of carcass parts over distances as short as several hundred meters may have been the rule, rather than the exception, for Plio-Pleistocene hominids (O'Connell, 1997; see also Lupo, 1993, p. 22–23; Potts, 1991; Rose and Marshall, 1996).

Figure 4 overlays medium bovid skeletal element data from Bed I and FxJj 50 on Stiner's (1994, pp. 253–254, 261) log-log regression for medium ungulate assemblages accumulated by four different predators. Mapping the Plio-Pleistocene assemblages onto Stiner's data has reduced the strength of the overall relationship [compare Stiner's (1994, p. 262) $r = -0.740$, $n = 22$, to the present $r = -0.62$, $n = 29$], though it remains significant ($P < 0.001$). When I included a dummy variable in the regression (Sincich, 1990, p. 677) to assess the significance of the Plio-Pleistocene sites as a categorical group, the relationship appeared to be much stronger ($r = -0.75$; $n = 29$) and was significant ($P < 0.001$) (Table III). The relationship between anatomical content and anatomical completeness at the Plio-Pleistocene sites is similar to Stiner's control cases, but with some significant differences in the relative proportions of skeletal elements. Given the age of the Olduvai and Koobi Fora sites, as well as the taphonomic uncertainties that arise from comparing sites from such diverse

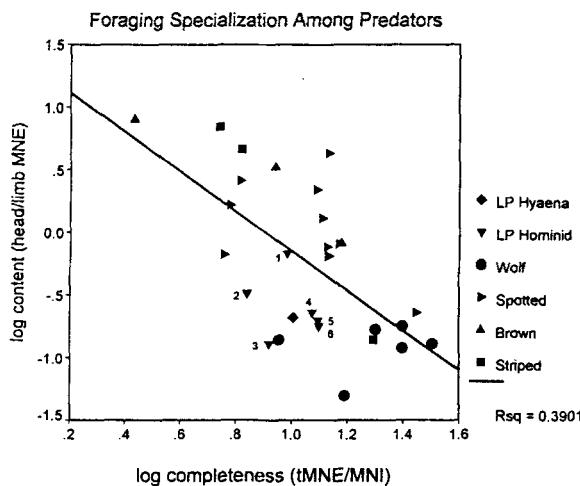


Fig. 4. Overlay of Plio-Pleistocene cases on Stiner's (1994, p. 261) log-log regression of anatomical content (head/limb MNE) by anatomical completeness (tMNE/MNI). The regression concerns medium bovids collected by various carnivores. Comparative carnivore data from Stiner (1994). Plio-Pleistocene data from Bunn (1982, 1986) and Potts (1988). Sites: (1) FLKNN-3; (2) DK; (3) FxJj 50; (4) FLK North 6; (5) FLKN-1-2; (6) "Zinj."

contexts, the correspondence with Stiner's (1994) data is quite remarkable and yields a few surprising results.

The distribution of the Plio-Pleistocene sites toward the middle of the regression suggests that Plio-Pleistocene hominids were engaging in some form of scavenging. The Plio-Pleistocene sites are most comparable to the range of scavenging strategies employed by the spotted hyaena, suggesting that early hominids may have engaged in a similar range of strategies. Spotted hyaenas are both formidable social predators and efficient scavengers and capitalize on both early and late carcass access times in various ecological situations (Kruuk, 1972; Mills, 1989, 1990). Thus, both relatively early and relatively late carcass access times may characterize the Plio-Pleistocene sites. The key difference between the spotted hyaena and the Plio-Pleistocene hominid sites is that the latter consistently fall below the regression line. This pattern indicates a greater proportion of limb elements, as well as less complete carcasses, in the Plio-Pleistocene sites. The striped and brown hyaena control cases present a contrasting pattern: all fall above the regression line and show a clear emphasis on head elements.

Table III. Log-log Regression of Anatomical Content by Anatomical Completeness^a

Total population				Dummy Variable for Plio-Pleistocene sites ^b			
Multiple R	-0.62459	Multiple R	-0.75935				
R ²	0.39012	R ²	0.57661				
Adjusted R ²	0.36833	Adjusted R ²	0.54525				
SE	0.48011	SE	0.40736				
Variables in the equation							
Variable	B	SE B	β	T	P	Variable	B
LGCOMP	-1.583678	0.374209	-0.624593	-4.232	0.0002	LGCOMP	-1.739171
(Constant)	1.431966	0.406472	3.523	0.0015		DUM	-0.612506
						(Constant)	1.739810
							0.356250
							4.884
							0.0000
							P

^aData for regression from Stiner (1994, pp. 250–270), Potts (1988), and Bunn (1982, 1986).

^bIncluding a dummy variable in the regression assessing the importance of the Plio-Pleistocene sites as a categorical group.

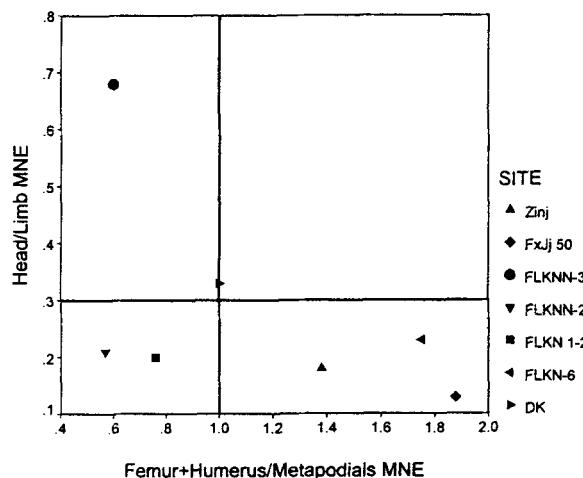


Fig. 5. A scatterplot of anatomical content (head/limb MNE) against a ratio of upper-limb/lower-limb MNE (femur + humerus/metapodials MNE). Higher meat yields are suggested by higher ratios of upper to lower limbs. Reference lines indicate expected ratios for complete carcasses. Data from Bunn (1982, 1986) and Potts (1988).

Only FLKNN-3 comes close to overlapping with the strategies employed by modern brown and striped hyaenas.

Figure 5 highlights some more specific features of the proportional representation of head and limb elements in the Olduvai sites and FxJ 50. As in Fig. 4, the ratio of head to limb elements in transported faunal assemblages may identify extremes of carcass access times; higher ratios of head to limb elements may indicate later carcass access times. The relative frequencies of upper-limb ("meaty") and lower-limb ("non-meaty") elements may provide another measure of carcass access times (Binford, 1979, 1984; Blumenschine and Madigral, 1993; Metcalfe and Jones, 1988; Monahan, 1996); one that more clearly separates the early from intermediate stages of consumption (Stages 1–3 and 4–5 in Fig. 2). Upper-limb elements consist of the humeri and femora; lower limb elements consist of the metapodials (Monahan, 1996). Higher upper- to lower-limb ratios may indicate earlier carcass access times.

The majority of the Plio-Pleistocene sites is clearly limb dominated (low head/limb MNE), suggesting that very late carcass access was not common (see also Binford, 1981; Bunn, 1982; Bunn and Kroll, 1986; Marean *et al.*, 1992; Potts, 1983, 1988). The one exception is FLKNN-3, which shows both a high relative frequency of head elements and a low relative fre-

quency of "meaty" limb elements; very late carcass access may have prevailed at this site. The remaining sites may be distinguished on the basis of upper- and lower-limb element representation. FxJj 50, FLK North 6, and FLK "Zinj" show a predominance of "meaty" limb elements. The evidence suggests that carcass access times may have been early at these sites (Stages 1-3), when greater amounts of meat were still available. In contrast, FLKNN-2 (a hyaenid accumulation) and FLKN 1-2 show a predominance of "non-meaty" limb elements, suggesting later carcass access times (Stages 4-5), but perhaps not as late as at FLKNN-3. The frequencies of head, upper-limb, and lower-limb elements at DK are consistent with the selection of elements in proportion to their natural abundances in complete carcasses. Thus, the evidence from DK also may indicate early carcass access times.

The conclusions that carcass access times may have been earlier at FxJj 50, FLK North 6, FLK "Zinj," and DK, and later at FLKNN-2, FLKN 1-2, and FLKNN-3, are compatible with detailed studies of bone damage and skeletal part representation at some of the sites (Bunn and Kroll, 1986; Oliver, 1994; Potts, 1982, 1983, 1988; see also Blumenschine, 1995). For example, frequencies of hominid and carnivore bone modification from FLK "Zinj" indicate that hominids had consistently earlier access to "meaty" limb elements (Oliver, 1994). Blumenschine (1995) reached similar conclusions on the basis of percussion mark and tooth mark frequencies, emphasizing that "passive modes" of carcass acquisition prevailed at FLK "Zinj." Inferred carcass access times, however, do not clearly specify the potential forms of interspecific competition encountered on the Plio-Pleistocene landscape or hominid tactics for coping with other large carnivores. I next turn to patterns of lithic tool reduction and raw material transport for addressing these questions. Independently of the faunal patterns discussed above, lithic technological data may reflect upon the character and intensity of early hominid movement around the ancient landscape.

Early Hominid Mobility

Questions of early hominid mobility may be addressed from several alternative perspectives. Variability in the use of different raw material types (i.e., lavas, quartzite) is the main focus of the following analysis. In general, raw material studies may reveal the distances over which raw materials were moved as well as the quantities and forms involved (see Harris and Herbich, 1978; Isaac, 1981; Kelly, 1992; Kuhn, 1991, 1995; Nelson, 1991; Potts, 1994; Toth, 1982; Toth and Schick, 1994). Such information is perhaps most revealing of the magnitude of early hominid mobility. Raw

material studies, combined with evidence on the character and intensity of tool reduction, may provide information about mobility tactics used to bring lithic materials and carcasses together (see Torrence, 1983, 1989; Kuhn, 1995, pp. 24–25). The following analysis is developed in several steps. First, I examine differences in the amounts of quartzite and lava artifacts present in the various assemblages (see also Leakey, 1971; Potts, 1988). Second, I examine differences in the pattern and intensity of quartzite and lava core reduction, focusing primarily on flake–core ratios. Third, I turn to bivariate regression models to identify stable patterns of “on-site” core reduction. This analytical step is based on the assumption that a predictable relationship will emerge between flake and core frequencies if cores are reduced only “on site.” Finally, I present an analysis of residuals from the regression models as a means of categorizing levels of deviation from expected “on-site” flake–core ratios. I argue that variable levels of hominid transport of flakes and cores in and out of foraging sites underlie the observed deviations in flake–core ratios and that levels of flake and core transport provide a proxy measure for levels of tactical mobility.

At Olduvai, quartzites and lavas combined make up more than 95% of the raw materials recovered (Table IVa). The quartzites derive from a localized outcrop (Naibor Soit) roughly 2 km north of the FLK localities and 2–3 km northwest of DK (Hay, 1976; Potts, 1988, p. 241). The lavas originate from the Lemagrut, Olmoti, Ngorongoro, and Sadiman volcanoes, on the margins of Olduvai Gorge, but are locally available from alluvial fans approximately 2 km to the east of the main gorge (Hay, 1976; Potts, 1988, p. 241). DK is directly associated with a lava outcrop at the site (Leakey, 1971; Potts, 1988).

Quartzite artifacts outnumber lava artifacts at “Zinj,” FLK North 6, and FLKN 1–2, while lavas dominate at FLKNN-3 and DK (Table IVa) (Leakey, 1971; Potts, 1988, p. 238). However, lava is clearly the dominant raw material by weight at all the Olduvai sites (Potts, 1988, p. 238). Lava artifacts outnumber quartzite artifacts at Koobi Fora, in most cases representing well over 95% of the recovered specimens (Table IVb) (Toth, 1982). The one deviation from the general pattern at Koobi Fora is FxJj 50, where raw materials other than lava constitute nearly 15% by number of the assemblage. The predominance of lavas at the Koobi Fora sites may reflect the abundance of these materials in stream channels in the area (Bunn *et al.*, 1980; Toth, 1982). FxJj 1, 3, 10, and 63 appear to have been situated several kilometers from workable raw material sources, whereas FxJj 50 is located at or near the raw material source (Toth, 1982, pp. 23–28).

These general contrasts in raw material representation both within the Olduvai Basin and between Olduvai and Koobi Fora suggest that there were differences in the way quartzite and lavas were treated by Plio-Pleistocene

Table IV. Percentages of Stone Raw Material Types by Number and Weight from Four Bed I Sites and by Number from FLKN 1-2 and the Koobi Fora Sites^a

Olduvai	DK		FLKNN-3		FLK "Zinj"		FLK North 6		FLKN 1-2	
	n	Weight (g)	n	Weight (g)	n	Weight (g)	n	Weight (g)	n	Weight (g)
Total (n)	1162	93,858	70	13,755	2647	72,403	116	12,012	1205	
% lava	76.4	94.8	52.9	89.9	9.5	72.3	17.3	62.9	30.7	
% quartzite	23.3	5.1	47.1	10	90.2	27.6	80.2	36.9	69.2	
% other	0.3	0.1	0	0	0.1	0.1	2.5	0.4	0.1	
b										
Koobi Fora	FxJj 1	FxJj 3	FxJj 10	FxJj 50	FxJj 63					
Total (n)	124	117	311	1,436	754					
% lava	96.8	96.8	99.4	85.2	99.6					
% quartzite	0	0	0	1.4	0					
% other	3.2	3.2	0.6	13.4	0.4					

^aData from Leakey (1971), Potts (1988, p. 240), and Toth (1982, p. 32).

hominids. Some of these differences may in fact reflect patterns of early hominid tactical mobility. To explore this possibility I address two related questions: Were lavas and quartzite treated differently only at the scale of core reduction? Or were they also treated differently at the scale of transport in and out of particular sites? I include as cores artifacts designated choppers, discoids, polyhedrons, heavy-duty scrapers, and protobifaces (see Leakey, 1971; Toth, 1982). Oldowan technology certainly was not designed and maintained (i.e., curated) in the senses that apply to more recent hominids (Binford, 1979; Kuhn, 1995; Nelson, 1991; Shott, 1996). As a consequence, Oldowan core reduction "strategies" probably are not all that informative about early hominid mobility. Transport of raw materials around the landscape, however, may bear on fine-scale variations in early hominid land-use. Short-term transport of raw materials to meet the constraints of time-stressed activities is of particular interest (Torrence, 1983, 1989). Yet the nature and intensity of raw material transport often depend on the nature and intensity of core reduction. Resource transport decisions are based not only on distances between procurement and destination sites, but also on the complexity of the raw material packages and the way that those packages are divided up prior to transport (Metcalfe and Barlow, 1992). Thus, questions of core and flake transport around the Plio-Pleistocene landscape cannot be addressed until we explore the nature of Oldowan core reduction.

The effects of raw material variability on core reduction are evident from a comparison of both flake–core ratios and typological variation across the assemblages. Table V presents data on core, flake, and shatter frequencies by raw material type. While some of the assemblages are exceedingly small when broken down by raw material type, there do appear to be some consistent patterns across sites. In particular, flake–core ratios seem to be consistently lower for lava raw materials than for quartzites. Lava flake–core ratios at Koobi Fora are similar to, if slightly higher than, those at Olduvai. The quartzite flake–core ratio from FxJ 50 is most similar to the lava artifact patterns at both Olduvai and Koobi Fora. Lava flake–core ratios at Olduvai and Koobi Fora range from less than 1 to 24 flakes per core. Quartzite flake–core ratios at Olduvai display a broad range of values, from approximately 10 flakes per core to more than 90 flakes per core. Compared to lava, it would appear that quartzite was reduced "on-site" much more intensively.

There are several potential explanations for the observed differences in lava and quartzite flake–core ratios. First, the differences could relate to the distinct fracture properties of the two raw materials. For example, quartzite may shatter more readily along cleavage planes. It is possible that there would be little or no observed difference between lava and quartzite flake–core ratios if we could control for the quartzite cores that shattered

Table V. Frequency of Cores, Flakes, and Shatter and Flake-Core Ratios at Olduvai Bed I and Koobi Fora Sites^a

Site	Material	Cores (<i>n</i>) ^b	Flakes (<i>n</i>)	Shatter (<i>n</i>)	Flake/Core
FLK North 6	Lava	4	3	0	0.8
"Zinj"	Lava	15	111	72	7.4
FLKNN-3	Lava	4	8	3	2.0
DK	Lava	139	598	405	4.3
FLKN 1-2	Lava	92	52	95	0.6
FxJj 50	Lava	53	416	754	7.8
FxJj 1	Lava	5	27	88	5.4
FxJj 3	Lava	1	24	89	24.0
FxJj 10	Lava	13	93	203	7.2
FxJj 63	Lava	25	235	691	9.4
FLK North 6	Quartzite	1	92	77	92.0
"Zinj"	Quartzite	26	2221	2002	85.4
FLKNN-3	Quartzite	0	28	26	
DK	Quartzite	16	198	149	12.4
FLKN 1-2	Quartzite	11	113	582	10.3
FxJj 50	Quartzite	4	11	5	2.8

^aData from Leakey (1971), Potts (1988), and Toth (1982).^bCores include choppers, discoids, polyhedrons, heavy duty scrapers, and protobifaces.

during reduction. While data separating core shatter from flake shatter are not available from the published literature, a strong positive log-log relationship between the shatter and the flakes across all sites ($r = 0.86$) indicates that flake populations increase in a predictable manner with shatter populations. As a consequence, it may not be necessary to correct for shatter frequencies when comparing lava and quartzite flake–core ratios.

The second hypothesis holds that the difference between lava and quartzite flake–core ratios stems from more extensive "on-site" reduction of quartzite. If so, then I would expect quartzite to be used more frequently for manufacturing polyhedrons and discoids; these core-tool types display mean flake scar counts of 7.1 and 8.8, respectively (Potts, 1991). In contrast, I expect that lava would be used more frequently to manufacture choppers and heavy-duty scrapers; these core-tool types display mean flake scar counts of 5.4 and 6.4, respectively (Potts, 1991). This appears to be the case at the Olduvai sites. For example, 10 of the 12 (83%) polyhedrons and discoids at FLK "Zinj" are made on quartzite, while 16 of the 25 (64%) choppers and heavy-duty scrapers are made on lava. Quartzite also appears more frequently as heavily reduced and battered spheroids/subspheroids (Schick and Toth, 1994, pp. 440–441). Anvils, hammerstones, and battered nodules and blocks, on the other hand, are made predominantly of lava

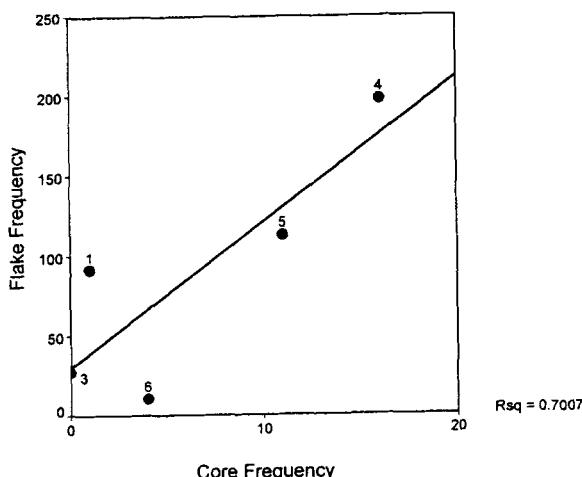


Fig. 6. Regression showing the relationships between quartzite flakes and cores at Olduvai and Koobi Fora. Site numbers: (1) FLK North 6; (3) FLKNN-3; (4) DK; (5) FLKN 1-2; (6) FxJj 50. FLK "Zinj" not included. Data from Leakey (1971), Potts (1988), and Toth (1982).

(Leakey, 1971, p. 264; Schick and Toth, 1994, p. 440). These patterns strongly suggest that quartzite was reduced very differently than lava.

While the differences in the extent of lava and quartzite reduction may relate to some currently unknown performance characteristics of the materials, the patterns and extent of Oldowan core reduction probably do not directly reflect upon levels of mobility: It takes relatively little time to reduce a given volume of stone raw material to hundreds of unstandardized flakes and pieces of shatter. Consequently, core reduction in itself is not likely to have been a limiting factor in bringing tools and food resources together at particular localities.

The third hypothesis holds that variation in lava and quartzite flake-core ratios might arise from a dynamic flow of flakes and cores in and out of sites (Isaac, 1983, p. 14; Schick, 1987; Toth, 1982). Movement of raw materials in and out of sites may also bear more directly on questions of early hominid tactical mobility. Separate flake–core regressions for quartzite (Fig. 6) and lava (Fig. 7) provide one means of assessing how well core frequencies predict flake frequencies and may also provide a measure of the intensity of "on-site" core reduction.⁴ The relationship between lava

⁴The FLK "Zinj" quartzite assemblage was identified as an outlier in preliminary analyses and is not included in the quartzite regression.

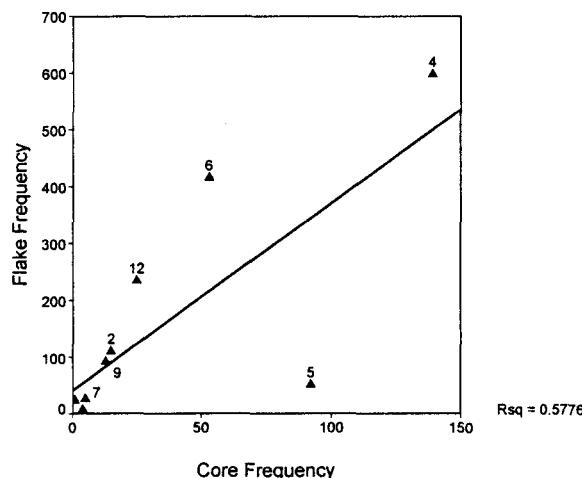


Fig. 7. Regression showing the relationships between lava flakes and cores at Olduvai and Koobi Fora. Site numbers: (4) DK; (5) FLKN 1–2; (6) FxJj 1; (9) FxJj 10; (12) FxJj 63. FLK North 6, FLKNN-3, and FxJj 3 are clustered near the origin. Data from Leakey (1971), Potts (1988), and Toth (1982).

flakes and cores is significant at $P < 0.05$, whereas the relationship for quartzite flake and cores is significant only at $P < 0.08$ (Table VI). The latter result is likely related to the sample size ($n = 5$) and could be improved with the addition of other sites to the analyses.

As expected, the regressions illustrate the tendency for quartzite to be more heavily reduced than lava (quartzite, $y = 30.28 + 9.08x$; lava, $y = 40.79 + 3.30x$). Certainly, the strong correlations between flake and core frequencies suggest that a fair amount of core reduction was taking place “on-site.” The strength of the relationship is not in itself a revelation, but something we should expect given that flakes necessarily derive from cores. It is curious, however, that core frequencies do not explain more of the variation found in flake populations. The frequency of quartzite cores explains approximately 70% of the quartzite flake frequencies ($r^2 = 0.701$), whereas lava cores explain only about 58% of the variation in lava flake frequencies ($r^2 = 0.578$) (Table VI). Thus, it seems that quartzite and lava flakes occur in frequencies both above and below what would be expected given strictly “on site” core reduction.⁵ I suggest that the unexplained vari-

⁵The observed differences in flake–core ratios could also be a product of systematic variations in intensities of core reduction between the sites. Examination of the ratio of heavily reduced core forms (polyhedrons and discoids) to less reduced core forms (choppers and heavy-duty scrapers) for lava assemblages at five of the Bed I sites failed to turn up significant

Table VI. Regression Statistics for Flake–Core Frequencies at Olduvai and Koobi Fora by Raw Material Type^a

Lava flakes by cores					
Variable	B	SE B	β	T	P
CORES	3.302	0.999	0.760	3.307	0.011
(Constant)	40.786	56.194		0.726	0.489
Variables in the equation					
Variable	B	SE B	β	T	P
CORES	9.081	0.427	0.837	2.650	0.077
(Constant)	30.279	30.420		0.995	0.393
Quartzite flakes by cores					
Variable	B	SE B	β	T	P
CORES	5				
Multiple R	0.837				
R ²	0.701				
Adjusted R ²	0.601				
SE	47.1365				
Variables in the equation					
Variable	B	SE B	β	T	P
CORES	5				
Multiple R	0.837				
R ²	0.701				
Adjusted R ²	0.601				
SE	47.1365				

^aData from Leakey (1971), Potts (1988) and Toth (1982).

ance in flake frequencies is the result of movement of cores or flakes in and out of the various sites (see Isaac, 1983; Schick, 1987; Toth, 1982, pp. 279–286). The distribution of residuals from each of the two regressions provides some elaboration of this interpretation.

Regression residuals provide a means of quantifying the degree to which individual assemblages deviate from the flake–core ratios predicted by the regressions (see Sincich, 1990, pp. 690–696). I decided to focus only on the magnitude of deviations from expected values in analyzing the quartzite and lava flake–core residuals, ignoring the particular direction of the deviations. The alternative of inspecting the direction of the residuals leads to difficult questions that involve modeling complex combinations of

correlations with flake–core ratios or regression residuals. While more rigorous confirmation of this pattern awaits a larger sample size, it appears that the intensity of core reduction is not responsible for the observed discrepancies in flake–core ratios. Moreover, systematic variations in core sizes are an unlikely source of the observed discrepancies since there are no clear size trends among the Bed I core types as a whole (Potts, 1991, pp. 159–160).

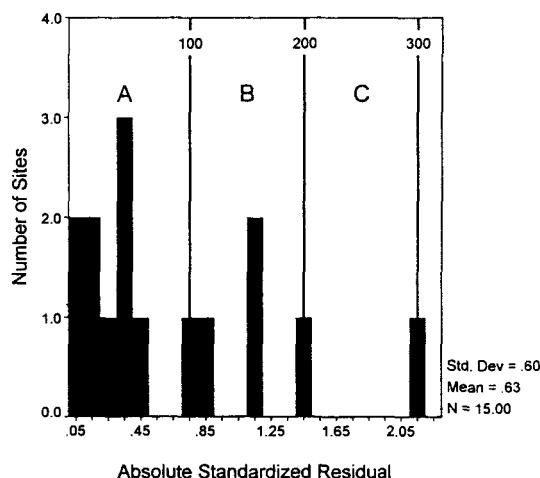


Fig. 8. Histogram of the combined absolute standardized residuals from the quartzite and lava flake–core regressions. The combined distribution falls into three zones, labeled A, B, and C, respectively. Data from Leakey (1971), Potts (1988) and Toth (1982).

flake and core transport events into and out of sites. In all practicality it is impossible to decipher whether observed flake–core ratios are the product of the movement of flakes, the movement of cores, or some combination of the two (see Isaac, 1983; Schick, 1987; Toth, 1982). However, by examining the absolute values of the regression residuals it is possible to assess the magnitudes of these transport events without having to specify which artifact types were involved, or whether the movement was in or out of the sites.

Acknowledging the small number of cases involved ($n = 15$), the majority of residuals clusters between 0 and 0.5 standard deviation as expected (9 of 15 sites) (Fig. 8). Beyond the primary peak, the residuals fall into two additional zones characterized by increasing discrepancies between flake and core frequencies. These three zones are labeled A, B, and C and are equivalent to discrepancies of < 100 artifacts, 100 to < 200 artifacts, and 200 to < 300 artifacts, respectively. The three residual zones may be interpreted in the following ways: Zone A represents assemblages where the numbers of flakes most resemble expected values for “on-site” core reduction. Zone B represents assemblages where a flake frequencies are not explained solely by “on-site” core reduction. Zone C represents assemblages where flake frequencies are largely unanticipated by “on-site” core reduction. Thus, zones A, B, and C may represent decreasing levels of “on-

Table VII. Absolute Standardized Residuals (ASR)
Grouped According to Magnitude and Raw
Material Type^a

Site	Material	ASR	Zone
FxJj 10	Lava	0.07	A
FxJj 3	Lava	0.14	A
FLK Zinj	Lava	0.15	A
FxJj 1	Lava	0.22	A
FLKNN-3	Lava	0.33	A
FLK North 6	Lava	0.37	A
DK	Lava	0.71	B
FxJj 63	Lava	0.80	B
FxJj 50	Lava	1.44	C
FLKN 1-2	Lava	2.11	C
FLK Zinj ^b	Quartzite	—	A
FLKNN-3	Quartzite	0.05	A
FLKN 1-2	Quartzite	0.36	A
DK	Quartzite	0.48	A
FLK North 6	Quartzite	1.12	B
FxJj 50	Quartzite	1.18	B

^aStandardized residuals are used to facilitate comparison between quartzite and lava regression results.

^bFLK "Zinj" was arbitrarily assigned to residual zone A.

site" core reduction and increasing levels of raw material transport through the various sites.

It is clear from these analyses that lava and quartzite are not equally represented in the analytical groupings (Table VII). Lava assemblages are found in all three zones. The lava assemblages from "Zinj," FLKNN-3, and FLK North 6 fall into zone A, or the lowest degree of raw material movement. The lava assemblage from DK falls into zone B, or moderate movement of raw materials. The lava assemblages from FLKN 1-2 and FxJj 50 fall into zone C, or the most extensive movement of raw materials. In contrast, quartzite assemblages fall only into zones A and B—low to moderate degrees of raw material movement. The quartzite assemblages from FLKNN-3, FLKN 1-2, DK, and perhaps "Zinj" are represented in zone A.⁶ FLK North 6 and FxJj 50 quartzite assemblages are found in zone

⁶The quartzite assemblage from FLK "Zinj" was arbitrarily assigned to zone A on the basis of several lines of evidence. The high quartzite flake–core ratio at FLK "Zinj" favors "on-site" core reduction as the best characterization of raw material usage patterns there. The quantity of quartzite moved to "Zinj" (~20 kg), as well as the sheer quantity of shatter (>2000 pieces) (Potts, 1988), also implies an "on-site" focus.

B. These patterns further underscore the differences in the way that lavas and quartzite were utilized; lavas may have been the favored raw material for activities involving tool transport, whereas quartzite may have been favored for activities needing more time for “on-site” core reduction.

At the Olduvai and Koobi Fora sites considered here, hominids apparently employed highly variable flake and core transport tactics. This variability is expressed not only in terms of concrete differences in the quantities of materials moved to the sites, but also in the intensities of flake and core transport represented. Placed in the context of hominid foraging tactics, the observed differences in the intensity of raw material movement may signal varying levels of tactical mobility. This inference is based on a series of interrelated expectations. In particular, how a site scores in terms of “on-site” focus may serve as a proxy for the risk or distances involved in hominid foraging forays. More intensive movement of flakes and cores, and a corresponding “off-site” focus, may signal higher levels foraging risk and higher levels of mobility aimed at getting tools to “time-stressed” activities (e.g., early carcass access) (see Potts, 1991; but also Rose and Marshall, 1996). For example, pilfering a fresh carcass from a hyaena might hinge on getting “ready-to-use” implements to the acquisition site rapidly, without much logistical preparation *en route*. Elevated levels of mobility are implied in such situations because of the high frequency and magnitude of movement necessary for foragers successfully to locate, acquire, transport, and safely consume the carcass under heavy competitive pressure (see Hoffer and East, 1993). Having lithic technology “on hand” is an integral part of these mobility tactics. Low-intensity movement of flakes and cores and a corresponding “on-site” focus, on the other hand, may signal low levels of mobility and, perhaps, the absence of “time-stressed” or high-risk activities. For example, relatively unimpeded access to fresh carcasses would provide hominids with more time for transporting cores and raw material (e.g., manuports) and more time for “on-site” tool manufacture. Lower levels of tactical mobility are implied in such situations because the frequency and magnitude of movement may not have been critical to carcass acquisition and because lithic raw materials could have been acquired in unstressed procurement forays.

In sum, the evidence presented in this study suggests that relatively high levels of mobility may be associated with lava tools at FLKN 1–2 and FxJj 50. Intermediate levels of mobility may be associated with lava tools at DK and quartzite tools at FLK North 6 and FxJj 50. Finally, low levels of mobility may be associated with lava tools at FLK “Zinj,” FLK North 6, and FLKNN-3 and quartzite tools at FLK “Zinj,” FLKNN-3, FLKN 1–2, and DK.

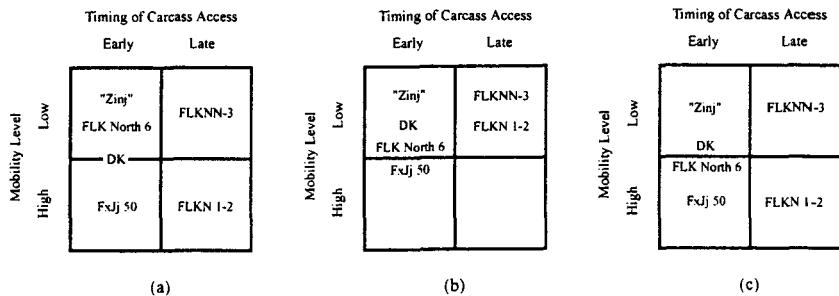


Fig. 9. Synthesis of archaeological data for the timing of carcass access and levels of tactical mobility at the Olduvai Bed I sites and FxJj 50. (a) Summary for lava artifacts. (b) Summary for quartzite artifacts. (c) Composite model selecting the highest level of mobility indicated by either lava or quartzite.

DISCUSSION

The first goal of this study is to explore archaeological data for the timing of carcass access and early hominid mobility, and it is clear that both were situationally highly variable. The second goal of this study is to relate the conclusions about the timing of carcass access and levels of tactical mobility to possible forms of interspecific competition and the sizes of early hominid foraging groups as laid out in Fig. 2. The inferred carcass access times and levels of mobility are presented for lava and quartzite separately and as a general model choosing the highest level of mobility indicated by either lava or quartzite (Fig. 9). The following interpretations focus on the general model and, at this stage, are merely hypotheses to be tested in future research.

- Early hominids may have practiced interference tactics at FxJj 50 (Cell C in Fig. 2). Early carcass access and high levels of mobility appear to have been "stressed" at this site. Early hominid activities in the vicinity of this site may have been organized around the group. Group organization may have been necessary to ensure effective defense of carcasses or to facilitate the pilfering of fresh carcasses from other large carnivores.
- Also potentially representing a high competition foraging context is FLKN 1-2. However, at this site it appears that exploitative competition may have prevailed (Cell D in Fig. 2). Relatively late carcass access appears to be paired with high levels of mobility at this site. Early hominid activities at FLKN 1-2 may have been organized around the individual. Individually organized mobility

may have been necessary to ensure greater areal coverage in the search for previously ravaged carcasses.

- Low-competition foraging contexts are suggested at FLK "Zinj." The timing of carcass access and mobility appear to have been relatively unstressed at this site (Cell A in Fig. 2). In such contexts, both group and individual organizations may have prevailed. FLK North 6 and DK may represent intermediate levels of foraging risk (between Cell A and Cell C in Fig. 2). Relatively early carcass and moderate levels of mobility are indicated at these sites. Early hominid activities at FLK North 6 and DK occasionally may have been organized around the group for interference strategies, but also may have seen more flexible social organizations when given access to fresh carcasses in low-risk contexts.
- A more marginal foraging context may characterize FLKNN-3. Later carcass access and low levels of mobility are suggested at this site. The organization of foraging groups seems unlikely in this case. Such marginal conditions could arise in extremely high-risk contexts where hominid interference and exploitative tactics were ineffective compared with other large carnivores. Alternatively, the marginal conditions inferred for FLKNN-3 may suggest that other resources were the primary focus of subsistence activities. In this case, it would be difficult to ascribe group or individual organizations to the hominids that occupied this site.

CONCLUSIONS

The inferences developed in this paper concerning hominid–carnivore competitive interactions, early hominid mobility, and the size of hominid foraging groups need not imply complex behavioral or social mechanisms (*cf.* Kuhn, 1995, p. 35). On the contrary, the kinds of behavioral and social flexibility envisioned here are characteristic of many nonhuman primates and carnivores (Chapman and Wrangham, 1993; Hoffer and East, 1993; Standen and Foley, 1989; Stiner, 1994; Wrangham *et al.*, 1993; see also Foley, 1984; Kaplan and Hill, 1992). Recent paleoanthropological research has started to develop more flexible interpretations along these lines (e.g., Blumenschine *et al.*, 1994; Potts, 1994; Rose and Marshall, 1996). And, like these other studies, it is not the intention of this paper to supplant models of early hominid behavior such as the stone cache hypothesis (Potts, 1988), routed foraging (Binford, 1981, 1984) or central place foraging (Isaac, 1978, 1984; Rose and Marshall, 1996). Rather, this paper may highlight some important links between these models and suggests that each may be in-

formative in different ecological contexts (see also Blumenschine *et al.*, 1994, p.206). For example, the inferred low competition contexts and minimal constraints on individual and group organizations at "Zinj" are consistent with some conceptions of early hominid central place foraging (Isaac, 1978, 1984; but see Rose and Marshall, 1996); without significant pressure from competing carnivores, early hominids could have foraged as individuals or in small groups, according to the tasks at hand, and safely transported resources to dependents waiting at central locations.

In contrast, the high competition contexts and group foraging tactics inferred at FxJj 50 are consistent with models of stone cache exploitation (Potts, 1988); under pressure from competing carnivores, groups of early hominids could have rapidly exploited stone caches for expedient tools, executed initial butchery at the acquisition site, and transported carcass elements back to the caches for further processing. Group defense of the carcass portions may have been necessary at such sites, followed by site abandonment and movement to safer locations (e.g., sleeping trees) (but see Rose and Marshall, 1996). DK and FLK North 6 may fall somewhere between the "unstressed" conditions at "Zinj" and the "stressed" conditions at FxJj 50. As such, these sites may be intermediate between central place foraging and stone cache use. Early hominids foraging in such contexts may have emphasized group organization only when faced with competitive pressure from other carnivores.

The marginal carcass exploitation and very high levels of competition that may have prevailed at FLKNN-3 accord well with models of early hominid routed foraging (Binford, 1981, 1984). Early hominids in the course of foraging for plant foods, or moving between necessary resources such as water holes and sleeping trees, may have individually encountered previously ravaged carcasses from which they could scavenge low-utility elements. In this case, the nature of site use and resource transport is not so much attuned to high-risk contexts as it is "embedded" in other low-risk activities (*sensu* Binford, 1979).

FLKN 1-2 may indicate similarly high levels of competition but a different tactic on the part of hominids for dealing with them. Rather than relying on chance carcass encounter "embedded" within other activities, individual hominids may have focused on extensive, broad search patterns, and exploitative use of dispersed, low-quality carcass parts. Interestingly, the stone cache hypothesis also is consistent with this inferred foraging organization—individuals quickly mining preexisting caches of flakes and cores before returning to the search.

To summarize, it is possible to envision a wide range of behavioral tactics, flexibly employed on ancient Plio-Pleistocene landscapes. Such flexible tactics could have played out differently over space and time, resulting

from the movement of a given hominid species between different habitats or in response to seasonal and long-term changes in the environment. The flexibility of such foraging tactics casts earlier models of early hominid behavior in a different light. Rather than implying that Plio-Pleistocene hominids were going through radical organizational shifts as they moved across different landscapes, this study suggests that aspects of routed foraging, stone cache exploitation, and central place foraging could be implemented as short-term tactics in particular ecological contexts. The degree of flexibility in Plio-Pleistocene hominid behavior suggested here also has implications for the origin and evolution of human behavior. Of particular interest is how flexible foraging tactics involving mobility and sociality arose and how selection operated on these behaviors once they were established. Future research focusing on a range of other discrete variables of early hominid behavioral ecology may provide additional tests of the model outlined above, as well as tests of more inclusive questions in hominid evolutionary ecology.

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