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Flaked Stones and Old Bones: Biological and Cultural Evolution at the Dawn of Technology

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ABSTRACT The appearance of Oldowan sites ca. 2.6 million years ago (Ma) may reflect one of the most important adaptive shifts in human evolution. Stone artifact manufacture, large mammal butchery, and novel transport and discard behaviors led to the accumulation of the first recognized archaeological debris. The appearance of the Oldowan sites coincides with generally cooler, drier, and more variable climatic conditions across Africa, probably resulting in a net decrease in woodland foods and an increase in large mammal biomass compared to the early and middle Pliocene. Shifts in plant food resource availability may have provided the stimulus for incorporating new foods into the diet, including meat from scavenged carcasses butchered with stone tools. Oldowan artifact form varies with clast size, shape, raw material physical properties, and flaking intensity. Oldowan hominins preferred hard raw materials with good fracture characteristics. Habitual stone transport is evident from technological analysis, and raw material sourcing to date suggests that stone was rarely moved more than 2–3 km from source. Oldowan debris accumulation was spatially redundant, reflecting recurrent visitation of attractive points on the landscape. Thin archaeological horizons from Bed I Olduvai Gorge, Tanzania, were probably formed and buried in less than 10 years and document hominin processing of multiple carcasses per year. Transport beyond simple refuging behavior is suggested by faunal density at some site levels. By 2.0 Ma, hominin rank within the predatory guild may have been moderately high, as they probably accessed meaty carcasses through hunting and confrontational scavenging, and hominin-carnivore competition appears minimal at some sites. It is likely that both *Homo habilis* sensu stricto and early African *H. erectus* made Oldowan tools. *H. habilis* sensu stricto was more encephalized than *Australopithecus* and may foreshadow *H. erectus* in lower limb elongation and some thermoregulatory adaptations to hot, dry climatic conditions. *H. erectus* was large and wide-ranging, had a high total energy expenditure, and required a high-quality diet. Reconstruction of *H. erectus* reproductive energetics and socioeconomic organization suggests that reproductively active females received assistance from other group members. This inference, combined with archaeological evidence for acquisition of meaty carcasses, suggests that meat would have been a shared food. This is indirectly confirmed by nutritional analysis suggesting that the combination of meat and nutritionally dense plant foods was the likely diet fueling body size increase and encephelization in *Homo*. Most discussion of Oldowan hominin behavior and ecology, including that presented here, is based on materials from a few sites. There is a critical need to analyze additional large, primary-context lithic and faunal assemblages to better assess temporal, geographic, and environmental variability in Oldowan behavior. Yrbk Phys Anthropol 47:118–164, 2004.

Two salient features distinguishing humans from the other living primates are the extent to which culture is used to deal with adaptive problems, and the relatively high proportion of vertebrate tissue in the human diet. It is of no surprise that the Oldowan archaeological sites have been of interest to paleoanthropologists and laypeople alike, as they provide the first concrete evidence of hominin material culture, as well as bone damage documenting the butchery of an enormous range of animals, literally from hedgehogs to elephants (Fernandez-Jalvo et al., 1999; Potts, 1988). Beginning ca. 2.6 million years ago (Ma) and continuing to 1.6 Ma, Oldowan artifacts are found at sites in eastern, southern, and northern Africa (Fig. 1). Cores were struck to produce sharp-edged flakes. One demonstrable use of these artifacts was animal butchery, but they may have been used to work wood and process plant foods

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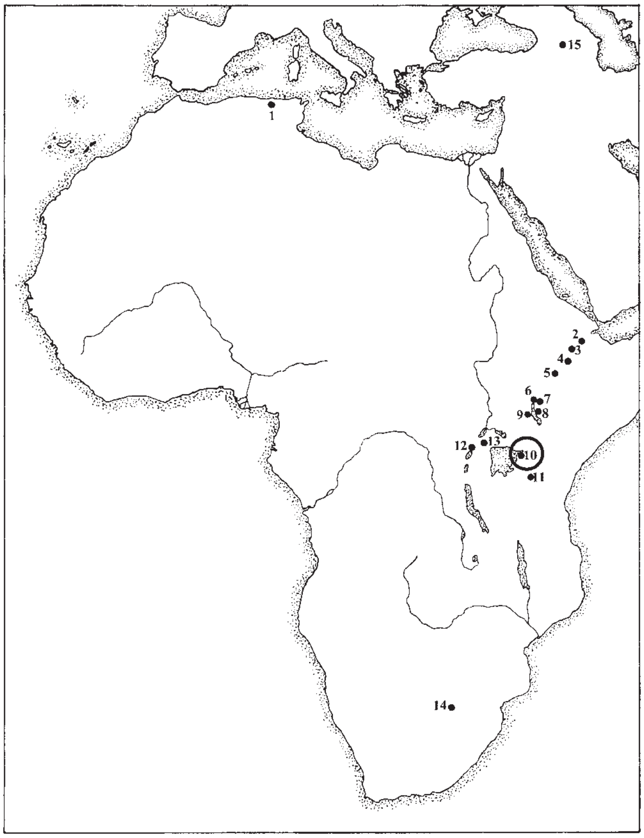

Fig. 1. Location of sites mentioned in text and in Table 1. 1, Ain Hanech; 2, Hadar; 3, Gona; 4, Middle Awash; 5, Melka Kunture; 6, Omo; 7, Fejej; 8, Koobi Fora; 9, West Turkana; 10, Kanjera South (circled); 11, Olduvai Gorge; 12, Senga; 13, Nyabusosi; 14, Sterkfontein; 15, Dmanisi. Redrawn from Isaac, (1997, p7).

as well. Artifacts older than 1.6 Ma in Africa are now commonly referred to as the Oldowan Industry within the Oldowan Industrial Complex (type site Olduvai Gorge; Isaac, 1984; Leakey, 1971). The term Oldowan is applied to this ancient technology, to the artifacts produced by these technological practices, and to the sites where these artifacts are found. Here I will also use this term in referring to the hominin producers of artifacts (i.e., Oldowan hominins).

Since 1995 I have been codirecting the Homa Peninsula Paleoanthropological Project (HPPP), an interdisciplinary team of paleontologists, archeologists, and geologists investigating the late Pliocene and Pleistocene deposits on the peninsula in southwestern Kenya (Behrensmeyer et al., 1995; Ditchfield et al., 1999; Plummer et al., 1999). Of interest here is the Oldowan occurrence we discovered at Kanjera South, which, based on biostratigraphy and magnetostratigraphy, is approximately 2.0 Ma (Table 1) (Behrensmeyer et al., 1995; Ditchfield et al., 1999). Excavation through sediments from an ephemerally flowing system of small, shallow channels, probably in a lake margin context, has recovered multiple levels of stone artifacts and associated fauna (Plummer et al., 1999). The 175-m^2 Excavation 1 is the largest excavation to date, and has yielded approximately 3,000 fossils and 4,500 artifacts with three-dimensional (3D) (N, E, and Z) coordinates from a 1-m-thick sequence, exclusive of materials from spit bags and sieving. This represents the first substantial Oldowan excavation with both artifacts and fauna outside of Olduvai Gorge, Tanzania. Data collection is well underway, with aspects of the lithic technology and zooarcheology being investigated by two doctoral students (David Braun, Rutgers University, and Joseph Ferraro, UCLA, respectively). I will be referring to research at Kanjera periodically throughout this review, to provide an example of a current, hypothesis-driven investigation of Oldowan hominin behavior and ecology from a site-based perspective.

THE TIMING AND DISTRIBUTION OF THE OLDOWAN

Oldowan occurrences are best known from East Africa, and sites in the 2.0–2.6-Ma range are found exclusively in this region (Table 1 and references therein; Fig. 1). Important late Pliocene localities include the Omo Shungura Formation, Gona region, and Hadar in Ethiopia, and West Turkana and Kanjera in Kenya. Whether the inception and earliest usage of Oldowan tools were restricted to East Africa, or whether behaviors forming Oldowan sites were more broadly distributed across Africa, is at this point unclear. Between 1.6–2.0 Ma, Oldowan sites were found in North (e.g., Ain Hanech, Algeria), South (e.g., Sterkfontein, South Africa), and East (e.g., Olduvai Gorge, Tanzania) Africa (Table 1). The recovery of a comparable technology to the Oldowan at Dmanisi, Georgia, at approximately 1.7 Ma suggests that the earliest travelers out of Africa brought the Oldowan tool kit with them (Gabunia et al., 2001).

The Developed Oldowan Industries A, B, and C, the Karari Industry, and the Acheulean Industry follow the Oldowan in time (Harris and Isaac, 1976; Isaac, 1984; Leakey, 1971). The Developed Oldowan contains broadly the same range of artifacts as the Oldowan sensu stricto, but with greater emphasis on scrapers, protobifaces, and spheroids. The Karari and Acheulean Industries each contain new artifact classes (Karari scrapers in the Karari Industry, and handaxes and cleavers in the Acheulean) made on large flake blanks (Harris and Isaac, 1976; Isaac and Harris, 1997; Ludwig and Harris, 1998). Developed Oldowan sites overlap the Acheulean in time and space within Africa, and may represent activity variants of this industry (Clark, 1970). These industries clearly developed from the Oldowan, but are distinguished from it technologically and temporally and so are beyond the scope of this review. Here the term Oldowan only refers to the technology from 1.6–2.6 Ma, exclusive of the Developed Oldowan.

TABLE 1. Major Oldowan occurrences[1]

Locality	Excavation	Age (my)	Excavation size (m^2)	Number of excavated artifacts	Raw material	Excavated terrestrial vertebrate fossils (NISP)[2]	Geomorphological and paleoenvironmental settings	Representative references
Gona, Ethiopia	Kada Gona 2–3–4	2.58–2.63	NR	21	B, T	0	Streambank or adjacent floodplain	Roche, 1996; Roche and Tiercelin, 1980
	West Gona 1	2.4	10	19	B, T	5	Streambank or adjacent floodplain with seasonal flooding	Harris, 1983; Harris and Capaldo, 1993
	EG10	2.5–2.6	13	667	T>70%	0	Floodplains close to stream channel margins	Semaw et al., 1997; Semaw, 2000
	EG12	2.5–2.6	9	444	T>70%	0	Floodplains close to stream channel margins	Semaw et al., 1997; Semaw, 2000
	OGS-6	ca. 2.6	NR	NR	NR	Surface fossil with cut marks	Bank of ancestral Awash River	Semaw et al., 2003
	OGS-7	ca. 2.6	2.6	265	La, T, R, C	34	Bank of ancestral Awash River	Semaw et al., 2003
Hadar, Ethiopia	AL 666	2.33	2.5	14	B, C	3	Predominantly open, with wetlands and bushed or wooded grasslands and with trees close to a water source	Hovers et al., 2002; Kimbel et al., 1996
Middle Awash, Ethiopia	Hata Mbr, Bouri Fm	2.5	NR	0	Not applicable	Several fossils with stone tool damage	Broad, grassy, featureless margin of a shallow freshwater lake	de Heinzelin et al., 1999
West Turkana, Kenya	Lokalalei 1 (GaJh5)	2.34	67	417	Predominantly lava	>3,415	Near intersection of ephemeral basin-margin streams and meandering, axial, ancestral Omo river	Kibunjia, 1994
	Lokalalei 2C (LA2C)	2.34?	17	2,067	Predominantly B, P (10 types)	239	Near intersection of ephemeral basin-margin streams and meandering, axial, ancestral Omo river; open environment on alluvial plain, with patches of bushes or forest along ephemeral river	Brown and Gathogo, 2002; Roche et al., 1999
Omo Shungura Fm, Mbr E, Ethiopia	Omo 84 (stratigraphic position unclear)	2.4–2.5 Ma?	NR	200	Q (B, C)	Present, found *below* artifacts	Distal edge of fluviatile levees, behind gallery forests bordering open savanna	Howell et al., 1987
Omo Shungura Fm, Mbr F, Ethiopia	FtJi 1	2.3–2.4 Ma	18	367	Q (C, L)	Present, derived context	Deposited in braided stream system	Howell et al., 1987; Merrick and Merrick, 1976
	FtJi 2	2.3–2.4 Ma	22	224	Q	0	Meandering stream system, distal edge of fluviatile levee, open floodplain between riparian forest and open savanna	Howell et al., 1987; Merrick and Merrick, 1976
	FtJi 5	2.3–2.4 Ma	8	24	Q	Present derived context	Deposited in braided stream system	Howell et al., 1987; Merrick and Merrick, 1976
	Omo 57	2.3–2.4 Ma	NR	30	Q (C, Qt)	Present	Deposited in braided stream system	Chavaillon, 1976; Howell et al., 1987
	Omo 123	2.3–2.4 Ma	NR	ca. 900	Q (C, Qt)	0	Meandering stream system, distal edge of fluviatile levee, open floodplain between riparian forest and open savanna	Chavaillon, 1976; Howell et al., 1987
Upper Semliki Valley, Democratic Republic of the Congo	Senga 5A	2.0–2.3	Not applicable, sediments disturbed and redeposited	723	Q (Qt)	4,400, but no definite behavioral association with artifacts	Not applicable, artifacts derived from Lusso Beds and subsequently redeposited	Harris et al., 1987, 1990

(*continued*)

TABLE 1. (Continued)

Locality	Excavation	Age (my)	Excavation size (m^2)	Number of excavated artifacts	Raw material	Excavated terrestrial vertebrate fossils (NISP)[2]	Geomorphological and paleoenvironmental settings	Representative references
Kanjera Fm (S), Kenya	Excavation 1	ca. 2.0 Ma	175	ca. 4,500 (under analysis)	Under analysis, but includes A, B, C, E, J, M, N, P, Q, Qt, R, S	>3,000 (under analysis)	Sites in wooded grassland to open grassland at basin margin with braided, intermittently flowing streams	Plummer et al., 1999; Braun, personal communication
Koobi Fora Fm, KBS Member	FxJj 82	ca. 1.77 Ma	95	624	B, (Q, C)	865	Floodplain sediments deposited as part of an alluvial system	Braun et al., 2003; Pobiner et al., 2004
	FxJj 10 (combined Isaac, Braun samples)	1.9	Approximately 100	555	B (I)	20	Artifact discard along bank of watercourse within fluviodeltaic floodplain setting	Harris and Capaldo, 1993; Isaac, 1997; Pobiner et al., 2004
	FxJj 3	1.9	44.5	120	L (I, Q OV)	237	Side of a slight depression (pool) along the course of a silted-up deltaic channel	Isaac, 1997
	FxJj 1	1.9	65	136	L (I, OV)	689	Shallow swale in tuff-choked channel surrounded by relatively flat swampy floodplain; pollen suggests open grassland and reed swamps with some gallery bush and trees	Isaac, 1997
Olduvai Gorge, Tanzania	FLK N 1–2	1.75	106	1,205	L, Qt	2,274	Lake margin	Bunn, 1986; Harris and Capaldo, 1993; Leakey, 1971; Potts, 1988; Rose and Marshall, 1996
	FLK N 3	1.75	105	171	L, Qt	1,254	Lake margin	
	FLK N 4	1.75	82	67	L, Qt	929	Lake margin	
	FLK N 5	1.75	115	151	L, Qt	2,210	Lake margin	
	FLK N 6	1.75	36	130	Qt, B/Ta, N (L, C)	>2,258	Lake margin	
	FLK 1 22 (Zinj)	1.76	290	2,647	Qt, VB, L (B/Ta, N, G, F)	ca. 40,172	Lake margin	
	FLK NN 3	1.76	209	72	B/Ta, N, L, Qt	>2,261	Lake margin	
	DK 2 and 3	1.86	233	1,163	B/Ta, VB, N, L, Qt (C,G,F)	>7,855	Lake margin	
Nyabusosi (Toro-Uganda)	NY 18	ca. 1.5	16	536	Q, C	None mentioned	From sequence of “fluvio-lacustrine” deposits	Texier, 1995
Fejej, Ethiopia	FJI locality	1.88	Surface	>150 from surface	Q (B)	Present on surface	Not stated	Asfaw et al., 1991
Melka-Kunture, Ethiopia	Gombore I B	ca. 1.7	200	ca. 8,000	B (O?)	Yes, amount not specified	Occupation of the banks of paleo-Awash River, riverine gallery forest	Chavaillon et al., 1979
Sterkfontein, South Africa	Member 5, Oldowan infill	1.7–2.0	Not; applicable cave infill	3,245	Q, Qt, C	Present, but perhaps not archaeological	Landscape near cave entrance wooded grassland to open grassland, locally moist catchment in immediate vicinity of cave	Bishop et al., 1999; Kuman, 1998; Kuman and Clarke, 2000
Ain Hanech, Algeria	Unnamed	ca. 1.8	54 m^2	1,232	E, C (S, Qt)	Present but not tallied	Alluvial floodplain cut by meandering river	Sahnouni and de Heinzelin, 1998; Sahnouni et al., 2002
El Kherba, Algeria	Unnamed	ca. 1.8	NR	270	E, C (S, Qt)	Present but not tallied	Alluvial floodplain cut by meandering river	Sahnouni and de Heinzelin, 1998; Sahnouni et al., 2002
Koobi Fora Fm, KBS Member	FxJj 82	ca. 1.77 Ma	95 m^2	624	B (Q, C)	865	Floodplain sediments deposited as part of alluvial system	Braun et al., 2003; Pobiner et al., 2004

[1] Artifact lithology abbreviations as follows: A, andesite; B, basalt; B/Ta, basalt/trachyandesite; C, chert/chalcedony/flint; E, limestone; F, feldspar; G, gneiss; I, ignimbrite; J, ijolite; L, lava indeterminate; La, latite; M, microgranite; N, nephelinite; OV, other volcanics; P, phonolite; Q, quartz; Qt, quartzite; R, rhyolite; S, sandstone; T, trachyte; Ta, trachyandesite; VB, vesicular basalt. Rare lithologies (<3%) are in parantheses. NR, not reported. Table after Potts (1991, p 156–157).

[2] NISP, number of identifiable specimens.

THE PALEOENVIRONMENTAL CONTEXT OF THE OLDOWAN

As reviewed in Potts (1998), environmental scenarios have long been used to provide context to major biological and cultural adaptations in hominin evolution. A particularly influential idea has been the turnover pulse hypothesis (Vrba, 1985, 1988), which in its original form argued that extinction and speciation events across multiple mammalian lineages (including the origins of the genera *Homo* and *Paranthropus*) were synchronized at around 2.5 Ma by a shift to more open environments in Africa "forced" by global cooling. This same environmental shift was argued to have precipitated the behavioral strategies leading to flake production, faunal and lithic transport, and the formation of debris accumulations on the landscape (Vrba, 1985; deMenocal, 1995). While the original hypothesis was modified (Vrba, 1995a,b), the potential linkage between unidirectional environmental change (Vrba, 1985) or environmental variability (Potts, 1996a) and Oldowan origins is important. A background to African environments and environmental change is thus necessary here.

There are a number of distinctive features of the African continent that undoubtedly influenced hominin evolutionary history. Continental uplift has exposed a variety of lithologies, resulting in spatially heterogeneous soils and vegetation types (Owen-Smith, 1999). Volcanism enriched soils in many regions, with leaching restricted by relatively low rainfall. The growth of nutritious grasses on these soils is a key characteristic of savannas, which cover much of sub-Saharan Africa and which form an important backdrop to hominin evolution. Savanna environments have extensive grass cover, with tree or bush cover ranging from isolated to nearly continuous (Harris, 1980). Continuous, treeless grassland also occurs, depending on the frequency of rain, fire, and grazing, as well as local soil conditions (Foley, 1987; Norton-Griffiths, 1979; Owen-Smith, 1999). This forage supports a high abundance and diversity of large grazing mammals. Rainfall varies in savanna areas from a low of about 250 mm to a maximum of about 1,500 mm per year. Precipitation is generally unevenly distributed between wet and dry seasons. Within regional landscapes, savanna may abut against forest with narrow transition zones. As savanna habitats grade into each other, climatic changes can lead to shifts along the gradient from open grassland to more wooded environments (or the reverse) (Foley, 1989).

Long-term climatic trends have clearly impacted the distribution of vegetation across Africa. These trends are incompletely understood but relate to large-scale processes such as orbital forcing, continental drift, shifts in oceanic currents, and orogeny (deMenocal, 2004; Denton, 1999; Potts, 1998). Changes are often expressed as a raising or lowering of global mean annual temperature, with estimates of change being based on marine sources, such as wind-blown dust (deMenocal, 1995) or oxygen isotope records (Shackleton, 1995). Changes in the annual temperature of the ocean or the proportion of aeolian dust in marine cores are then translated into changes in terrestrial environments, such as the increase in the proportion of C_4 plants (e.g., lowland tropical grasses) during cool dry intervals in the global climatic regime. Teasing out the pattern and process of global and regional climatic change and investigating the impact these changes had on the evolution of African terrestrial ecosystems have become an important endeavor to paleoanthropology.

The emergence of the Oldowan at approximately 2.6 Ma follows on the evolutionary heels of a successful group of hominins, the gracile australopithecines. The gracile australopithecines (genus *Australopithecus*) of the early and middle Pliocene are mainly known from East Africa (*Australopithecus anamensis*, 3.9–4.17 Ma; *A. afarensis*, 2.9–3.6 Ma; *A. garhi*, 2.5 Ma) and South Africa (*A. africanus*, 2.4–2.8 Ma), though a poorly known taxon was recently described from Chad (*A. bahrelghazali*) (Brunet et al., 1995; Johanson and White, 1979; Kimbel, 1995; Leakey et al., 1995; White, 1995, 2002). They share some general features, including locomotor repertoires combining terrestrial bipedality with a substantial amount of climbing (Leakey et al., 1995; Lovejoy, 1988; Stern, 2000; Stern and Susman, 1983; White, 2002) and thick enamel and large cheek teeth relative to *Ardipithecus ramidus* and extant African apes (White et al., 1994; Johanson and White, 1979). Gracile australopithecines are associated with environments that include moderate to substantial amounts of woodland (Andrews, 1989; Reed, 1997; Schoeninger et al., 2003; Vrba, 1985). Analysis of mandibular corpus size and robusticity, tooth size and morphology, dental topography, dental microwear, trace element analysis, and stable carbon isotope analysis suggest that *Australopithecus* diets had diverged from the living apes, with *A. afarensis* perhaps focusing on soft fruits but also incorporating nuts, seeds, and abrasive terrestrial foods (roots and rhizomes) requiring incisal stripping (Ryan and Johanson, 1989; Ungar, 2004). *A. africanus* is believed to have consumed a variety of C_3 plant products (fleshy fruits, seeds, and leaves), with stable carbon isotopic evidence indicating that on average 33% of its diet came from C_4 plants (e.g., grasses, sedges) or animals eating C_4 plants (Grine, 1981; Kay and Grine, 1988; Schoeninger et al., 2001a; Sponheimer and Lee-Thorp, 2003; Teaford and Ungar, 2000; Teaford et al., 2002; Ungar, 2004; Walker, 1981). *Australopithecus* was quite successful, was probably broadly distributed across sub-Saharan Africa, and persisted over one and one half million years from the early into the middle Pliocene (White, 2002).

Between 2.0–3.0 Ma, a number of significant high-latitude climatic changes, including the onset of major Northern Hemisphere glaciation, occurred

(Shackleton et al., 1984; Vrba, 1985, 1995a,b; de Menocal, 2004). While it is difficult to tease apart the influence of global climatic change from that of local and regional events (e.g., uplift and volcanism associated with the East African Rift System) (Hill, 1995; Partridge et al., 1995), a general consensus has emerged that changes in the global climatic regime did impact African terrestrial ecosystems in significant ways. The general pattern over the last 4 Ma appears to have been an overall cooling and drying trend that was punctuated by intervals of greater aridity that increased the proportion of open habitats as well as the heterogeneity of the responding ecosystems (Alemseged, 2003; Bobe and Eck, 2001; Bobe et al., 2002; Bobe and Behrensmeyer, 2004; Behrensmeyer et al., 1997; Cerling, 1992; deMenocal, 1995, 2004; Prentice and Denton, 1988; Vrba, 1985, 1995a,b; Wesselman, 1995; Wynn, 2004). An increase in xerophytic vegetation (including grass) relative to the early Pliocene seems to be reflected in morphological changes associated with the increased consumption of tougher and possibly more abrasive foodstuffs in many African large mammal lineages (e.g., equids, suids, elephantids, hippopotamids, bovids) (Turner and Wood, 1993; Wood, 1995). The movement of grazing fauna into Africa, and especially the dispersal of *Equus* across the continent from Eurasia around 2.3 Ma (Coppens and Howell, 1976), is concordant with this idea. Evolutionary change within the Homininae during the late Pliocene is coincident with and may be causally related to environmental change. The last gracile australopithecines (*A. africanus* and *A. garhi*) disappeared between 2.4–2.5 Ma, and *Paranthropus* and *Homo* made their first appearances between 2.3–2.7 Ma (Hill et al., 1992; Kimbel, 1995; Kimbel et al., 1996; Walker et al., 1986; White, 2002).

While there appears to have been an overall increase in the relative proportion of grass in floral communities in the late Pliocene, faunal change in the Turkana basin of Kenya and Ethiopia, arguably the best regional sample from Africa between 1–4 Ma, does not provide evidence of a discrete turnover pulse of speciation and extinction attributable to a single global climatic event (Behrensmeyer et al., 1997). Rather than being a static trend toward more open environments, or reflecting a single or small number of pulses of faunal turnover synchronized by global climatic change, the faunal record from the Turkana basin apparently documents significant shifts in the abundance of common families of mammals, episodes of high faunal turnover, and increases in the number and relative abundance of grasslands adapted mammals in multiple pulses (Bobe and Behrensmeyer, 2004; Wynn, 2004).

The increase of the grass component in the floral community may have added heterogeneity to the existing range of habitats rather than resulting in expansive grassland tracts (Cerling, 1992). Woodlands and forest persisted within the Turkana basin until about 2.0 Ma, and isotopic data from the Baringo basin, Kenya, do not record a dramatic expansion of grassland in the terminal Pliocene (Kingston et al., 1994). Rather, later Pliocene mammalian evolution may reflect the cumulative consequences of cooler, drier, and more variable climatic conditions linked to shifts in global climate in complex ways (Behrensmeyer et al., 1997; Potts, 1996a).

Several points are clear from the above discussion: late Pliocene environments in Africa remained complex, spatially heterogeneous mosaics of forest, woodland, bushland, and grassland, the proportions of which fluctuated over geologic time. Grasses and other arid-adapted vegetation often made up a greater proportion of the floral community than they did in the early and middle Pliocene. However, the increase in proportional representation of xerophytic vegetation should not be viewed as the replacement of closed canopy woodland with open grassland. African habitats grade from forest to open grasslands, with many intermediate habitat types (Harris, 1980). An increase in grasses may have largely taken the form of a net decrease in closed canopy woodlands and an increase in grassy woodlands, wooded grasslands, and bushland.

The question when assessing the paleoanthropological record is how the overall drying trend as well as variability in aridity over geologic time impacted hominin floral and faunal paleocommunities (and thus potential hominin food resources), both during generational time as well as geologic time. One way to begin addressing this question is to assess the relative impact that climatic change would have had on woody plant species distributions. Woody plants that are likely to have provided food to hominins (e.g., *Adansonia digtata*, baobab, providing fruit and seeds, and *Grewia* spp. providing berries and seeds) are widely distributed across Africa today (O'Brien and Peters, 1999; Peters and O'Brien, 1994). The distribution of woody plant species richness, including the richness of woody plants producing edible fruit, follows the pattern of variation in vegetation ecophysiognomy. Species richness increases from desert to semiarid vegetation, to shrubland, bushland, woodland, and forest. O'Brien (1993, 1998) and O'Brien et al. (1998) demonstrated that woody plant diversity in South Africa is well-described by rainfall amount and energy (heat/light), and that this relationship between climate and woody plant species richness can be applied elsewhere. Thus, local and global climatic factors that affect rainfall or temperature will directly influence the amount of woodland foods available to primates.

Competition for resources during the late Pliocene can thus be thought of as varying along different time scales, e.g., geologic time down to the annual seasonal cycle. During periods of increased global cooling and aridity, the relative reduction in deciduous shrubs and trees would have reduced the quantity, and spatial and temporal availability, of large, fleshy fruits, nuts, and seed pods, which were probably important components of the diets of early and middle Pliocene gracile australopithecines (Sept, 1986; Peters and O'Brien, 1981; Walker, 1981; Peters et al., 1984; Foley, 1987; Grine, 1981; Kay and Grine, 1988). As is found in relatively arid areas of Africa today, legumes, plants producing hard fruits and seeds, and bushes producing berries would have become better represented as rainfall decreased (Peters et al., 1984; Sept, 1986). Relative to the warmer, more humid periods when woodland plant resources would have been abundant, competition for resources from deciduous trees during the cool, dry portions of the global climatic cycle would have been high. Competition would have been further exacerbated by an increase in the seasonality of rainfall during arid periods. In modern African settings, the degree of seasonality is correlated with mean annual rainfall (Harris, 1980). As the amount of rainfall decreases, it tends to be less evenly distributed during the year, leading to periods of low primary productivity and thus plant food shortage (Altmann, 1998; Foley, 1987). While it is difficult to demonstrate the degree of seasonality of rainfall in the past, it seems likely that there were times when the dry seasons were periods of stress and heightened competition for resources, just as they are today. Certainly by 1.89 Ma, recurrent patterns of accentuated striae in *Theropithecus oswaldi* teeth are reflective of seasonal fluctuations in food availability over an annual cycle (Macho et al., 1996).

The increase in the proportional representation of grass in the floral community would have provided little in the way of food resources for hominins, but it did support a large community of grazing mammals. Primary productivity of tropical savanna is a bit more than half that of tropical woodland, but secondary (herbivore) productivity is nearly three times higher in savanna than in woodland (Leonard and Robertson, 1997, 2000). The biomass levels attained by wild herbivores in Africa greatly surpass large mammal biomass in other regions of the world today. Moreover, within Africa, grazing ungulate abundance is an order of magnitude greater than that of similarly-sized browsing ungulates, because graze has greater year-round accessibility relative to browse, and more of the plant production in grass-dominated environments is available for herbivore consumption (Leonard and Robertson, 1997; Owen-Smith, 1999).

Oldowan hominin habitat preference

Is it possible to situate Oldowan hominin activities within the spectrum of savanna habitats mentioned above? Paleoenvironmental inferences for hominin activities are frequently limited, as paleontological and archaeological sites are only preserved where sedimentation occurs. There are no primary context Oldowan sites in South Africa, and East African sites are found in fluvio-lacustrine settings, biasing our perspective to activities carried out in near-water contexts (Table 1). Faunal and pollen data, where they exist, invariably provide evidence of a range of savanna habitats, varying from woodland to patches of open grassland, which hominins may have freely ranged through, or within which they may have shown specific habitat preferences. Moreover, the depositional context of isolated hominin fossils may not provide a clear indication of habitat preference during life (White, 1988). As reviewed by Sikes (1994), there is little consensus regarding Plio-Pleistocene hominin habitat preferences in East Africa. Archaeological occurrences can provide evidence of hominin activities in specific paleoecological settings and of the broader paleocommunity that the hominins were part of (Bishop et al., in press; Plummer and Bishop, 1994; Sikes, 1994). Methods such as stable isotopic analysis of pedogenic carbonates and phytolith analysis can provide an indication of the paleohabitat in which archaeological accumulations were formed, if habitat boundaries did not shift repeatedly across the site during its depositional history. Archaeological fauna can provide an indication of the range of habitats available in the paleoecosystem, and may provide information about hominin foraging ecology.

As noted above, archaeological sites are frequently found in well-watered depositional settings that may have been wooded in the past. The Gona and Omo Shungura sites in Ethiopia probably formed in or near riparian woodlands (Howell et al., 1987; Harris and Capaldo, 1993). The oldest Oldowan sites in the Lake Turkana basin at 2.3 Ma tend to be low-density scatters lying between the toes of active alluvial fans from drainage systems feeding into the ancestral Omo River and the river itself (Rogers et al., 1994; but see Roche et al., 1999). These areas were thought to afford hominins trees for shade, food and shelter, water, and a convenient source of stones for tool production. Sites occur in lake margin settings between 1.8–1.9 Ma at both Lake Turkana and Bed I Olduvai Gorge, Tanzania, which also may have been wooded (Fernandez-Jalvo et al., 1998; Plummer and Bishop, 1994; Sikes, 1994).

Olduvai Gorge, Tanzania is the best-known locality in which the paleoenvironmental context of Oldowan archaeological occurrences can be assessed using both in situ archaeological fauna and stable isotopic data documenting the habitats present during site formation. Stable isotopic analyses of paleosol carbonates and associated organics from Bed I (1.75–1.98 Ma) and lower Bed II (ca. 1.74 Ma) Olduvai, for example, have documented archaeological occurrences in habitats ranging from riverine forest to grassy woodland (Sikes, 1994). The carbon isotopic values of Sikes (1994) on paleosol carbonates agree well with those obtained by Cerling (1992) and Cerling and Hay (1986) from paleosol carbonates from Beds I and II (excluding the Lemuta Member). In contrast to modern East African ecosystems with a large C_4 component, suids are consistently more abundant than equids at the Bed I Oldowan sites (Potts, 1988), and Bed I suid postcranial ecomor-

TABLE 2. Plio-Pleistocene hominin data, with humans and chimpanzees for comparison[1]

Taxon	Time span (Ma)	Cranial capacity	Mass (kg)		Body weight dimorphism	EQ	MQ	Representative localities
			Male	Female				
Pan troglodytes	Extant	410	49	41	1.20	2.0	0.9	
Australopithecus garhi	2.5	450						Bouri, Ethiopia
Australopithecus africanus	2.4–>2.8	452	41	30	1.37	2.7	2.0	Taung, Makapansgat, Sterkfontein, South Africa
Paranthropus aethiopicus	2.3–2.7	410						West Turkana, Kenya; Omo Shungura, Ethiopia
Paranthropus boisei	1.4–2.3	521	49	34	1.44	2.7	2.7	Olduval Gorge and Penlnj, Tanzania; Koobi Fora, Kenya; Omo Shungura and Konso-Gardula, Ethiopia
Paranthropus robustus	1.7	530	40	32	1.25	3.0	2.2	Kromdraai, Swartkrans, Drimolen, Gondolin, South Africa
Homo habilis	1.6–2.33	612	37	32	1.16	3.6	1.9	Omo and Hadar, Ethiopia; Olduval Gorge, Tanzania, Koobi Fora, Kenya; Sterkfontein, South Africa
Homo rudolfensis	1.9	752	60	51	1.18	3.1	1.5	Koobl Fora, Kenya; ?Uraha, Malawi
Early African *Homo erectus*	1.5–1.8	871	66	56	1.18	3.3	0.9	Koobi Fora and West Turkana, Kenya
H. sapiens sapiens	Extant	1,350	58	49	1.18	5.8	0.9	

[1] Data from McHenry (1994) and McHenry and Coffing (2000). Encephelization quotient (EQ) is calculated as brain mass divided by (11.22 × body mass$^{0.76}$). Megadontia quotient (MQ) is postcanine tooth area divided by (12.15 × body mass$^{0.86}$).

phology is suggestive of a woodland habitat preference (Bishop, 1994). While Oldowan hominins were undoubtedly utilizing woodland resources and forming sites within woodlands, the question of whether and how they used more open habitats has been difficult to assess, because these open settings have not been documented with isotopic or faunal evidence.

The ca. 2.0-Ma sediments at Kanjera South, Kenya, appear to sample the open contexts not yet documented at Bed I Olduvai, and demonstrate the formation of archaeological sites within them. As published in Plummer et al. (1999) and further substantiated with additional sampling, the Kanjera paleosol carbonates from within and below the archaeological horizons have $\delta\ ^{13}C$ values indicative of habitats within the range of wooded grassland to open grasslands. Analysis of the Excavation 1 faunal sample suggests that hominin activities were not formed within an isolated patch of C_4 vegetation, but that grass was a significant component of the regional plant paleocommunity. Antelopes from tribes that today live in open settings dominate the bovid sample. The proportions of bovids, equids, and suids recovered from Excavation 1 are similar to the proportions of these families in modern, C_4-dominated game reserves (Plummer et al., 1999; Potts, 1988) and contrasts with the Bed I faunal assemblages, where suids are consistently more abundant than equids (Potts, 1988). These results demonstrate that Oldowan hominins were not always limited by predation pressure to forming sites in woodlands, and suggests that they may have broadly utilized the habitats in their environment.

WHO MADE THE OLDOWAN TOOLS?

Associating the Oldowan with particular hominin taxa is a difficult task, particularly since its temporal range overlaps that of three genera (*Australopithecus*, *Paranthropus*, and *Homo*) and potentially eight different hominin species (Table 2). Stone tool usage has often been linked to the genus *Homo* in the literature (Leakey et al., 1964; Leakey, 1971; Stanley, 1992), but currently the oldest fossil definitively attributable to *Homo* (maxilla A.L. 666 from Hadar, Ethiopia, at 2.33 Ma) is nearly 300,000 years (Ka) younger than the first artifacts at ca. 2.6 Ma (Kimbel et al., 1996; Semaw et al., 2003). Either the antiquity of early *Homo* is underestimated (as suggested by fragmentary specimens possibly attributable to *Homo* at ca. 2.4 Ma from the Lake Baringo basin, Kenya (Sherwood et al., 2002) and the Omo Shungura Formation, Ethiopia (Suwa et al., 1996)), or a gracile australopithecine on the lineage to *Homo* formed the earliest archaeological accumulations. The youngest East African gracile australopithecine, *Australopithecus garhi*, is found in the same sediments as some of the oldest evidence of butchery with stone artifacts (2.5 Ma from the Bouri Formation, Middle Awash, Ethiopia; Asfaw et al., 1999; de Heinzelin et al., 1999). This has led some to speculate that *A. garhi* was the first stone tool-user and a likely ancestor to *Homo* (Asfaw et al., 1999; de Heinzelin et al., 1999; Semaw et al., 2003). However, there is too little paleontological evidence from the 2–3-Ma interval to be confident in this conclusion. In contrast, it is clear that *A. africanus* predates the oldest artifacts from South Africa, precluding this taxon from Oldowan artifact manufacture (Kuman, 1998).

The distribution of *Paranthropus* largely overlaps that of Oldowan archaeological occurrences in East and South Africa. Susman (1988, 1991) argued that *Paranthropus* was a stone tool user, and a likely accumulator of some Oldowan artifact concentrations. This remains a possibility, but an unlikely one. First, his argument hinges on hand bones from Swartkrans, South Africa, which morphologically provide evidence for refined manipulation and precision grasping necessary for stone tool manufacture. While their morphology is consistent with tool use, these hand bones are not unequivocally attributable to *Paranthropus robustus*. The Member 1 craniodental sample is dominated by *P. robustus* specimens, but *Homo* is also present. Recent taphonomic analysis suggests that the hominin postcranial fossils at Swartkrans were deposited through carnivore voiding (Pickering, 2001). Postcranials may therefore have had a separate taphonomic history from the hominin skulls and the Developed Oldowan tools at the site (Pickering, 2001), an argument against a simple probabilistic assignment of the hand bones to the craniodentally most common taxon (see also Trinkaus and Long, 1990). The use of Oldowan tools for a variety of pounding tasks is evident from pitting on utilized pieces (Leakey, 1971). The investment in large jaws and cheek teeth in the *Paranthropus* lineage would be developmental "overkill" if a tool kit allowing extra-oral processing of food was available. Finally, there is no perceptible change in the archaeological record after *Paranthropus* goes extinct, as might be expected if two parallel tool traditions were in place during much of the Plio-Pleistocene. *P. robustus* may indeed have used bones for digging into termite mounds (Backwell and D'Errico, 2001), but its association with the Oldowan seems doubtful.

H. erectus is the single definite stone tool user. Early African *H. erectus* (*H. ergaster* to some) appears by 1.8 Ma, prior to the development of the Karari or Acheulean Industries (Anton, 2003; Isaac, 1997). This taxon is known from Dmanisi, Georgia, shortly thereafter at ca. 1.7 Ma with a simple, Oldowan-like tool kit (Gabunia et al., 2001). This indicates that the transition to a body size approximating that of modern humans and the first known dispersal of hominins out of Africa occurred during the course of the Oldowan. Additional cranial material (e.g., occipital fragment KNM-ER 2598 from East Turkana, Kenya) may push the first appearance of this taxon back to 1.88–1.9 Ma (Anton, 2003; Feibel et al., 1989; Wood, 1991). Isolated postcranial elements from East Turkana, Kenya (e.g., femora KNM-ER 1472 and 1481a at 1.89 Ma, innominate KNM-ER 3228 at 1.95 Ma) provide further evidence of large-bodied *Homo* with femoral elongation back to nearly 2 Ma (Anton, 2003; Rose, 1984). Whether these isolated elements signify the emergence of *H. erectus* at 2.0 Ma or were drawn from an earlier form of *Homo* has been the subject of some debate (Kennedy, 1983; Trinkaus, 1984; Wood, 1992; Wood and Collard, 1999). In either case, barring the discovery of *H. erectus* at 2.6 Ma, it appears that evolutionary change in *Homo* is not synchronized with technological change.

The taxon ancestral to *H. erectus* would almost certainly have used stone tools. However, the phylogenetic relationships of fossils attributed to earliest *Homo* are problematic: some researchers recognize a single, variable taxon (*Homo habilis* sensu lato, age range of 1.6–2.33 Ma; Tobias, 1991a,b), while others suggest that the late Pliocene sample of *Homo* includes more than one species (Stringer, 1986; Wood, 1991). The division by Wood (1991, 1992)) of earliest *Homo* into a large, more megadont form (*H. rudolfensis*; 1.9 Ma and perhaps older) and a smaller form (*H. habilis* sensu stricto; 1.6–2.33 Ma) has been particularly influential (Dunsworth and Walker, 2002; Wood, 1992). Both of these taxa share with later *Homo* increased brain size relative to body weight (McHenry and Coffing, 2000; Wood and Collard, 1999) and possibly decreased masticatory size relative to body weight (Haeusler and McHenry, 2004; McHenry and Coffing, 2000; but see Wood and Collard, 1999). More recently, it was suggested that the genus *Homo* be defined starting with early African *H. erectus*, and that *H. habilis* and *H. rudolfensis* be transferred to *Australopithecus* (*A. habilis* and *A. rudolfensis*, respectively; Wood and Collard, 1999). A central tenet of this view is that the appearance of *H. erectus* marked a new adaptive grade in human evolution, and that specimens generally referred to as *H. habilis* sensu lato were more similar physically, behaviorally, and in their life history to australopithecines than they were to *H. erectus*. Inferred primitive limb proportions for OH 62, a *H. habilis* sensu stricto specimen from Olduvai Gorge, Tanzania, provided part of the justification for transferring *habilis* and *rudolfensis* into *Australopithecus* (Johanson et al., 1987; Wood and Collard, 1999). This partial skeleton was argued to have a humero-femoral ratio closer to *Pan* and *A. afarensis* than to *H. sapiens*, though the femur was too poorly preserved to provide an accurate length (Asfaw et al., 1999). A recent reevaluation of *H. habilis* limb proportions suggests that they were intermediate between *Australopithecus* and *H. erectus*, combining a human-like (long) lower limb with an australopithecine-like (long) forearm (Haeusler and McHenry, 2004). Small *H. erectus* specimens from Dmanisi, Georgia (Vekua et al., 2002), East Turkana and Olorgesailie, Kenya (Leakey et al., 2003; Potts et al., 2004), and Olduvai Gorge, Tanzania (Anton, 2004), demonstrate that *H. erectus* overlapped with *H. habilis* sensu stricto in size to a greater degree than was previously appreciated. Phylogenetic analyses of craniodental traits have linked *H. habilis* sensu stricto strongly with *H. erectus* (Lieberman et al., 1996; Strait et al., 1997), and the morphology of finds from Dmanisi, Georgia, and particularly cranium D2700, suggests a close relationship between these taxa (Vekua et al., 2002). It thus seems premature to move *habilis*, and presumably *rudolfensis* as well, into *Australopithecus*.

In summary, it seems unlikely that *Paranthropus* spp. or *A. africanus* manufactured Oldowan artifacts. The evidence for an ancestor-descendant relationship between *H. habilis* sensu stricto and *H. erectus* strongly argues that *H. habilis* manufactured Oldowan tools. *H. habilis* was probably forming archaeological occurrences by between 2.0–2.3 Ma, and both *H. habilis* and *H. erectus* were forming archaeological sites between ca. 1.6–ca. 2.0 Ma. This is significant, because archaeological sites from this overlap interval might ultimately provide subtle differences in environmental context, faunal acquisition strategy, and carcass yield, reflecting niche partitioning between these two taxa. Some of the features of the adaptive grade shift argued for *H. erectus* may be presaged in earlier *Homo* taxa. Whether *H. rudolfensis* used stone artifacts is impossible to judge at this point, as is the taxon responsible for the earliest archaeological assemblages between 2.3–2.6 Ma.

HOMININ TRANSFORMATIONS IN THE PLIO-PLEISTOCENE: OBSERVATIONS ON ENERGY, SIZE, AND DIET

A number of researchers have highlighted the significance of the transformation from an *Australopithecus* grade of hominin to *H. erectus* (Aiello and Key, 2002; Aiello and Wells, 2002; Aiello and Wheeler, 1995; McHenry and Coffing, 2000; Wood and Collard, 1999). This contrast is heightened by the 0.5-Ma or greater gap between these groupings, and disagreement over the taxonomic status of specimens attributed to *H. habilis* sensu lato. If *H. habilis* sensu stricto and *H. rudolfensis* are valid taxa, and if the analysis of Haeusler and McHenry (2004) is correct, then they would presage the transformation to *H. erectus* by: 1) lower limb elongation in *H. habilis* (unknown in *H. rudolfensis*), 2) possession of a protuberant nose with inferiorly directed nares in *H. habilis* (as signaled by the nasal morphology in KNM-ER 1813) and possibly, though less likely, in *H. rudolfensis* (Franciscus and Trinkaus, 1988), 3) a possible drop in body size dimorphism in both early *Homo* taxa to the level seen in *H. erectus*, 4) an increase in relative brain size (EQ; more pronounced in *H. habilis* sensu stricto), and 5) a decrease in relative postcanine tooth area (MQ) over the terminal gracile australopithecine taxa (*A. africanus* and *A. garhi*).

Lower limb elongation (a feature going back to at least 2.5 Ma based on taxonomically indeterminate fossils from Bouri, Ethiopia; Asfaw et al., 1999) might signal increased ranging, possibly related to shifts in habitat patchiness and food distribution (Haeusler and McHenry, 2004; Isbell et al., 1998). An elongated lower limb would also serve to assist with heat dispersion at high velocities (Wheeler, 1991, 1992, 1993), and a protuberant nose would assist in moisture retention, both useful adaptations to bouts of high activity in hot, dry environments. Estimates of neocortex size in *H. habilis* and *H. rudolfensis* suggest a larger social group size than in the australopithecines (Aiello and Dunbar, 1993), again possibly related to increased use of open habitats with attendant predation risks (Foley, 1987; Isbell, 1994). EQ increase coupled with a decrease in MQ relative to late *Australopithecus* is suggestive of increased dietary quality, with concomitant increases in energy expenditure and home range size (Leonard and Robertson, 1997; McHenry and Coffing, 2000).

Viewed in this way, *H. habilis* sensu stricto might be seen as a reasonable transition between *Australopithecus* and *H. erectus*: a relatively small-bodied hominin showing some adaptations to increased ranging in environments that were often relatively dry, and with a larger brain and higher-quality diet than *Australopithecus*. Maturation may have been slowed slightly relative to *Pan* and the gracile australopithecines (Bogin and Smith, 2000; but see Dean et al., 2001). Tool use would have provided access to rich food sources, including scavenged large mammal carcasses. *H. erectus* might then represent a further elaboration on this theme, with increased body size (itself potentially a consequence of more extensive ranging into open environments; Aiello, 1996), a reduction of forearm length to provide fully modern limb proportions, and (if they were not present earlier) a narrow pelvis, barrel-shaped chest, and gut reduction. The evidence for slower maturation relative to *Pan* and earlier hominins is stronger in *H. erectus* than *H. habilis* sensu stricto, but still not unambiguous (Bogin and Smith, 2000; Clegg and Aiello, 1999; Dean et al., 2001). Absolute (but not relative) brain size increased over *H. habilis*, and the area of postcanine dentition dropped dramatically, signaling a continued shift toward high-quality foods requiring less oral preparation. Relative to earlier hominins, there would have been an increase in energy requirements due to increases in body mass as well as brain enlargement, which would have been met by increased dietary quality and energy-sparing through gut reduction (Aiello and Wells, 2002) and reduction in the amount of skeletal muscle relative to other primates (Leonard et al., 2003).

Comparative data on primate and human hunter-gatherer energetics suggest that total daily energy expenditure rose from australopithecines to *H. erectus* by at least 40–45%, and if *H. erectus* had a human-style foraging strategy, by 80–85% (Leonard and Robertson, 1997). Relative energy expenditure and day ranges are both positively correlated with diet quality in anthropoid primates, suggesting that there was a large increase in energy expenditure in *H. erectus*, and that the taxon was more far-ranging than previous hominins (Leonard and Robertson, 1992, 1997). This appears true even when considering recently discovered, smaller-bodied *H. erectus* (Anton and Swisher, 2004). Increased size of offspring would have led to greater energy requirements during gestation and lactation than australopithecines. These may have been offset by decreasing the interbirth interval and reorganizing the economic division of labor within the group to assist mothers in feeding their weanlings and dependent children (Aiello and Key, 2002; O'Connell et al., 1999).

The large body size of *H. erectus* combined with its longer, more linear form would have provided benefits to both thermoregulation and water balance under hot, dry conditions (Wheeler, 1991, 1993; Ruff, 1991). Combined with its essentially modern nose configuration, it can be surmised that this taxon thermoregulated much as humans do, including prodigious sweating during bouts of high activity (Foley, 1987).

The behavioral ecology of bipedality in *H. erectus* was a tremendous shift from the australopithecine condition (Kramer, 2004). Its long legs may have been adaptations for increased daily range, increased maximum walking velocity, and increased dispersion of heat (Isbell et al., 1998; Kramer, 2004; Kramer and Eck, 2000; Wheeler, 1991, 1993). With their small body size and short legs, australopithecine females were well-adapted to relatively slow-speed foraging that required little burden-carrying besides infant transport. Both male and female *Homo erectus* were probably adapted for longer-distance and/or higher-speed travel and more efficient transport of heavier burdens than australopithecines (larger individuals carry heavy burdens more efficiently than smaller ones; Kramer, 1998). Children walk with less energetic efficiency than adults, and presumably *H. erectus* infants were either carried or left somewhere safe during adult foraging.

The emerging picture of *H. erectus* is of a creature that was large and wide-ranging, could efficiently transport burdens, had a high total energy expenditure, and ate a high-quality diet. Evidence of a thermoregulatory adaptation similar to humans (presumably including the same sweating capacity) suggests that they were active during the heat of the day, and by doing so could have minimized interactions with most large predators (Foley, 1987; Lewis, 1997). Femoral cortical bone thickness indicates that activity levels were high in early *Homo* (Ruff et al., 1993; Ruff, 2000), and the overall *H. erectus* body plan suggests that it shared a unique capacity with humans: the ability to endurance-run (Carrier, 1984; Hilton and Meldrum, 2004). Ruff et al. (1993) argued that high levels of femoral robusticity in early *Homo* reflect high activity levels, and that the decline in postcranial robusticity in *Homo* through the Pleistocene may reflect cognitive and technological advances, analogous to what has been argued for cheek tooth reduction through time. These high activity levels may have been related to subsistence practices, including hunting involving bouts of endurance running, which over time were mitigated by more energetically efficient hunting weaponry or strategies.

RESEARCH APPROACHES TO THE OLDOWAN

Crude "pebble tools" were documented in North Africa, East Africa, and South Africa (Biberson, 1967; Clark, 1970; Leakey, 1935; Toth and Schick, 1986) in the first half of the 20th century. The term "Oldowan" was first applied to artifacts from the oldest layers at Olduvai Gorge, Tanzania, and from Kanjera and Kanam West on the Homa Peninsula, Kenya (Leakey, 1935). Olduvai Gorge became the type-site of the Oldowan Industrial Complex (Leakey, 1971). The practice of exposing large, horizontal surfaces to investigate spatial patterning of archaeological materials and to relate these to prehistoric behavior was introduced to Africa by Mary and Louis Leakey in their Acheulean excavations at Olorgesailie, Kenya, in the 1940s (Isaac, 1977), and was widely adopted thereafter (e.g., Clark, 1969; Isaac, 1977; Leakey, 1971). Oldowan sites were initially viewed through strict analogy with hunter-gatherers, particularly the Kalahari San, and large, primary context assemblages were interpreted as campsites or home bases (Leakey, 1971; see below).

From the 1970s, research orientation shifted away from rigid ethnographic analogy toward hypothesis testing, and researchers began to consider Oldowan behavior in broader environmental and adaptive contexts (Binford, 1981; Isaac, 1984; Potts, 1988).

"Actualistic" studies, including artifact replication and use feasibility studies, studies of plant and animal resource availability in different modern ecosystems, and observations of factors conditioning resource transport, site formation, and food-sharing among modern hunter-gatherers emerged as important sources for generating data to interpret the paleoanthropological record (Binford, 1981; Blumenschine, 1986; Bunn et al., 1988; Capaldo, 1998; Hawkes et al., 2001; O'Connell et al., 1990, 1999, 2002; Selvaggio, 1998; Sept, 1994, 2001; Stahl, 1984; Tappen, 1995, 2001). Investigation of Plio-Pleistocene archaeological sites through excavation of relatively dense artifact distributions (sometimes called "maxisites") continued, but new research strategies emerged, including: 1) excavation of "minisites" believed to represent a single or few episodes of hominin activity; 2) "scatter between the patches" surface surveys which sought to investigate hominin activities from a landscape perspective, focusing more attention on the low-density scatters between maxisites; and 3) dispersed, generally small-scale excavations of "landscape distributions" of archaeological material, also attempting to investigate hominin discard behavior beyond the bounds of single sites (Blumenschine and Masao, 1991; Bunn et al., 1980; Isaac, 1997; Isaac and Harris, 1978; Isaac et al., 1981; Kroll, 1994; Leakey, 1971; Potts, 1994; Potts et al., 1999; Rogers, 1996; Stern, 1993, 1994).

Currently, excavations of Oldowan occurrences at Gona and Hadar in Ethiopia and Lokalalei and Kanjera in Kenya are "site-based," in that the units of analysis are artifacts and fossils drawn from individual sites or site complexes, rather than from landscape-wide distributions of archaeological debris. The Olduvai Landscape Palaeoanthropology Project (OLAPP, Rutgers University) is the sole Oldowan project carrying out a paleolandscape approach, though Upper Burgi and KBS Member archaeology at Koobi Fora, Kenya, is increasingly being viewed from a paleolandscape perspective (Pobiner et al., 2004).

Paleolandscape investigations of archaeological distributions postdating the Oldowan sensu stricto include FxJj43, Kenya, for the Karari (Stern et al., 2002), Peninj, Tanzania, for the Developed Oldowan (Domínguez-Rodrigo et al., 2002), and Olorgesailie, Kenya, for the Acheulean (Potts et al., 1999). There are relative advantages and disadvantages to each approach: site-based approaches may provide larger samples of artifacts and fossils in precise relationship to each other for refined technological analyses (e.g., refitting, determining reduction sequences), paleoecological analysis (pollen, isotopic, and micro- and macromammalian faunal analysis), and zooarchaeological analysis (mode of carcass acquisition, degree of carcass completeness, carcass processing strategies, and intensity of competition with carnivores at sites repeatedly visited by hominins), with more detailed contextual information linking materials together. The obvious disadvantage of the site-based approach is that it provides a narrow window to view Plio-Pleistocene hominin activities, and some of the dynamic nature of hominin landscape usage is lost. The paleolandscape approach may help assess the degree of spatial focus of hominin discard behavior and investigate the relationship between discard and resource distribution (Blumenschine and Peters, 1998; Potts et al., 1999), particularly if there is tight chronostratigraphic control over the target layer(s) of interest, excavations are situated and large enough to adequately sample the distribution of objects, variation in object density does not predominantly reflect variation in sedimentation rates across the landscape, samples of recovered objects are large enough to carry out technically rigorous analyses, and the distribution of resources of interest to hominins across the ancient landscape were stable over time and well-enough understood to allow interpretation of time-averaged artifact and faunal discard patterns. To date, most interpretations of Oldowan hominin behavior have been derived from site-based analyses and actualistic and ethnoarchaeological data, and these data sets will be emphasized here.

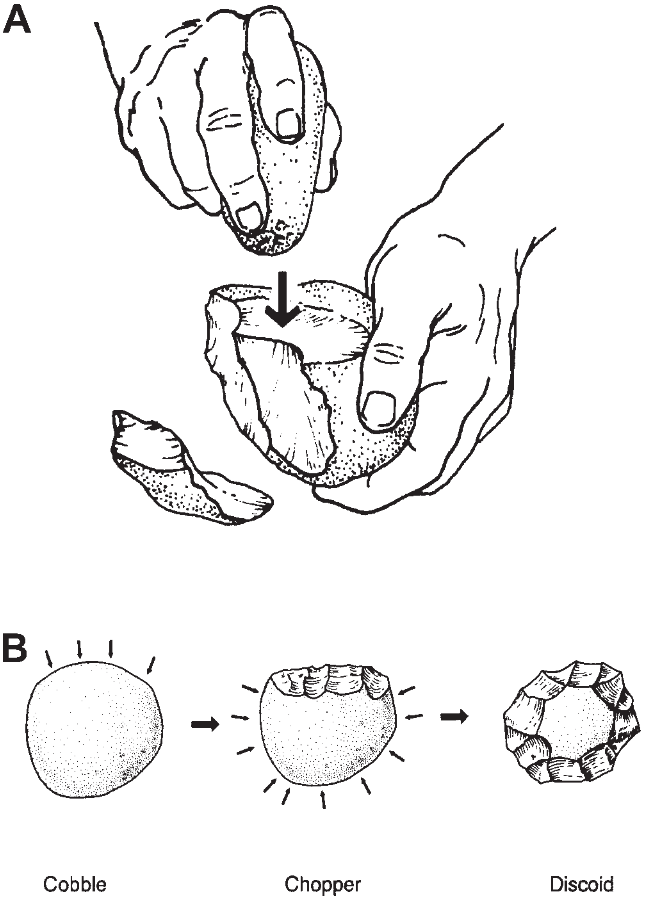

Fig. 2. **A:** Production of flakes through hard hammer percussion. Resultant core form is a chopper in typology of Leakey (1971). After Schick and Toth (1993, p 121). **B:** Much of variation in Oldowan core forms is continuous. Sequential removal of flakes around perimeter of a cobble transforms it from chopper to discoid. After Potts (1993, p 61).

OLDOWAN TECHNOLOGY

Artifact classification

Mary Leakey published the first formal description of Oldowan tools from Bed I and lower Bed II Olduvai Gorge, Tanzania (Leakey, 1966, 1971), creating a typology that is still widely referred to. Flakes were produced by using one stone (a hammer stone) to knock flakes off of another (a core) in a technique termed hard hammer percussion (Fig. 2). Cores were sometimes set on an anvil and struck from above (bipolar percussion) or fractured by throwing them against a hard substrate (Merrick and Merrick, 1976; Kuman, 1998; Roche, 2000). Leakey (1966, 1971)) classified hominin-modified lithics into three groups: tools, utilized material, and debitage. Tools were further subdivided into light-duty (e.g., retouched flakes) and heavy-duty (e.g., choppers) categories, based on whether mean diameter was less than or exceeded 50 mm (Leakey, 1971; Schick and Toth, 1993; Toth, 1985). Hammer stones, anvils, or flakes damaged through use were termed utilized pieces. Her debitage category included unmodified flakes, flake fragments, and other knapping debris. Manuports were natural stones transported and discarded without modification. Leakey (1971) believed that heavy-duty tools were the most significant component of the Oldowan "toolkit," that hominins shaped their tools with a clear idea of the desired end product, and that different tool forms were used for different tasks.

More recently, it was argued that the Oldowan was a simple but effective method of producing sharp flakes from stones, and that flakes, not cores, were often the desired end product (Keeley and Toth, 1981; Potts, 1991; Toth, 1985, 1987). Rather than following a mental template, Oldowan hominins relied on simple spatial concepts to coordinate flake production (Wynn, 1981; Wynn and McGrew, 1989). Core form was strongly influenced by the size and shape of raw material, its flaking characteristics, and flaking extent (Potts, 1991; Toth, 1985). While terms by Leakey (1971) are still used in discussing Early Stone Age (ESA) artifact assemblages, the terminology of Isaac (1984) and Isaac et al. (1981) avoids assumptions about artifact usage. In his scheme, stones from which flakes were removed are termed "flaked pieces" (FPs), flakes and other forms of flaking debris are termed "detached pieces" (DPs), and hammer stones are termed "pounded pieces" (PPs).

Stone tool function

Assessing the function of Oldowan artifacts is an indirect exercise. The co-occurrence of artifacts and fossils at localities such as DK, FLK NN, FLK, and FLK N at Bed I Olduvai Gorge were long thought to reflect hominin processing of animal tissue (Leakey, 1971). However, a direct relationship between artifacts and bones was only established with detailed, taphonomically oriented studies of Oldowan fauna (e.g., Bunn, 2001; Bunn and Kroll, 1986; Potts, 1988). Though disagreement remains over methodology (Bunn and Kroll, 1986; Potts, 1987), there is consensus that cut marks on bone reflect butchery and meat removal (Bunn, 1981; Potts and Shipman, 1981). Combined with percussion damage reflecting marrow extraction (Blumenschine, 1995; Oliver, 1994), cut marks demonstrate hominin processing of animal carcasses with stone artifacts. Processing of faunal materials remains the single clear example of Oldowan artifact function, with recent finds of butchered bones coincident with the first appearance of the technology at 2.5–2.6 Ma (de Heinzelin et al., 1999; Semaw et al., 2003). Otherwise, replicated artifacts have been used to assess the feasibility of carrying out tasks observed among living hunter-gatherers, such as woodworking, hide-slitting and -scraping, butchery, and nut- and bone-cracking (Jones, 1981; Schick and Toth, 1993; Toth, 1997). Many butchery and woodworking tasks were best conducted with simple flakes, highlighting the importance of DPs within the Oldowan. Some FPs were well-suited for heavy-duty activities, such as wood-chopping and bone-breaking. Though the processing of an array of plant and animal tissues was possible, there is little direct evidence linking Oldowan artifacts to specific tasks other than butchery and bone-breaking. Microwear analysis of a small sample of 1.5-Ma Karari artifacts from Koobi Fora showed that hominins (presumably *H. erectus* henceforth) were cutting meat, processing soft, siliceous plant materials (grasses or reeds), and working wood (Keeley and Toth, 1981). Phytoliths recovered from the edges of handaxes from the roughly coeval site of Peninj, Tanzania, also suggest woodworking (Domínguez-Rodrigo et al., 2001). This implies that hominins were making tools with other tools, a behavior rarely if ever observed among great apes (McGrew, 1992). It also highlights that some (perhaps a substantial proportion of) ESA material culture was made of wood and other perishable materials. As of yet, microwear and phytolith analysis has not been successfully applied to Oldowan artifacts, though microwear analysis is currently being attempted with the Kanjera artifact sample.

Degree of technological variability

Research at localities other than Olduvai Gorge has underscored the variability in Oldowan technology (Roche et al., 1999; Semaw et al., 1997) in terms of reduction sequences, proportions of different tool "types," raw material utilization, and perceived degree of technological "competency" (e.g., Chavaillon, 1976; Kibunjia, 1994; Kibunjia et al,. 1992; Roche, 1989; Roche et al., 1999). This has led some to posit a "pre-Oldowan" phase in the archaeological record from 2.0–2.5 Ma, characterized by a less sophisticated approach to artifact production. For example, Kibunjia (1994) argued that assemblages older than 2.0 Ma should be placed in the Omo Industrial Complex to highlight differences in flake production and technical competency before and after 2.0 Ma. Recently, Roche et al. (1999) emphasized the high degree of variability in technological competency in assemblages older than 2.0 Ma, arguing that later assemblages show more uniform evidence of a sophisticated grasp of flake production combined with refined motor precision and coordination. Others argue that archaeological sites from 1.6–2.6 Ma evince the same understanding of stone fracture mechanics and competency in flake production (Ludwig and Harris, 1998; Semaw, 2000; Semaw et al., 1997). These researchers noted that hominins from ca. 2.6-Ma sites at Gona, Ethiopia, had an understanding of stone fracture mechanics as sophisticated as that seen at ca. 1.8-Ma sites at Bed I Olduvai, Tanzania. Because assessment of assemblage "sophistication" is subjective, and differences due to blank shape, raw material type, and duration of flaking are important determinants of assemblage variation, there does not yet seem to be a compelling reason to erect different facies or industries for the first million years of the archaeological record.

Raw material selectivity

Oldowan hominins used a variety of lithic raw materials (Table 1). Quartz dominates the Fejej, Omo Shungura Fm, Nyabusosi, and Sterkfontein artifact samples. At Bed I Olduvai, quartzite and several types of igneous rock (e.g., basalt, trachyandesite, and nephelinite) were used. At Ain Hanech and El-Kherba, artifacts were predominantly made of limestone and flint (Sahnouni et al., 2002). At Kanjera, in contrast, a great diversity of raw materials was used, reflecting the geologic heterogeneity of the Homa Peninsula and surrounding environs (Le Bas, 1977; Plummer et al., 1999; Saggerson, 1952). At most other Oldowan sites, the dominant raw material(s) tend to be locally available igneous rocks. Chert is a common, though low-frequency, element in the Oldowan raw material repertoire. At the assemblage level, raw material variation is limited by local availability of appropriately sized raw materials with suitable fracture properties. It is clear that Oldowan hominins preferred hard, fine-grained raw materials that fractured well when impacted (Isaac and Harris, 1997; Leakey, 1971; Toth, 1985). Sites were often located at or near raw material sources, frequently stream channel conglomerates (Table 1), and hominins sometimes selected raw materials in the frequency they occurred in these conglomerates (Isaac, 1997; Schick and Toth, 1993).

Several sites hint at preferential use of specific raw materials. At the East Gona sites EG10 and EG12 in Ethiopia, hominins appear to have selected one raw material (trachyte) over others (Semaw, 2000; Semaw et al., 1997). The small (n = 258) artifact sample from the nearby site of OGS-7 includes 12% chert debitage (Semaw et al., 2003). Chert is a rare element in the local conglomerates, and so may have been selectively utilized and transported by hominins. At the Bed I Olduvai sites, Leakey (1971) found that heavy-duty tools (FPs) were commonly made of lava, while quartzite frequently dominated the light-duty tool, utilized flake, and debitage (DP) categories. The Bed I manuport sample is dominated by lava stones (Kimura, 2002; Potts, 1988). This may suggest that quartzite was used somewhat differently than lava; transported pieces were flaked relatively rapidly, with percussion leading to the disintegration of cores and the production of many flakes and core fragments. These sharp shards may have been preferred for light-duty cutting tasks. The lack of the appropriate amount of lava debitage to account for the cores at many sites may indicate that lava cores were flaked elsewhere before being deposited on-site, and that lava core forms may have been preferred for certain heavy-duty tasks (Leakey, 1971).

The technology at Kanjera South provides insights into hominin behavior in the late Pliocene. Although flakes and debris dominate the assemblage, core forms from Kanjera South are distinct from some other Oldowan assemblages. Unlike the dominance of unifacial forms seen at some sites at Gona, Ethiopia (Semaw, 2000), the emphasis on bipolar forms in the Omo Industries (Chavaillion, 1976; Merrick and Merrick, 1976), and the greater emphasis on choppers in the Olduvai assemblages (Leakey, 1971), Kanjera flaked-piece assemblages seem to be focused on radial, discoidal, and polyhedral forms. Large flakes are often reutilized as cores, and polyfacial forms are prevalent in some raw materials. No one core production mode (Roche, 2000) dominates the assemblage. Curation beyond what is commonly associated with an Oldowan assemblage is suggested by the presence of core rejuvenation flakes and intentionally retouched flakes, where the retouch is unidirectional and continuous, and tends to be concentrated on one edge. The assemblage is characterized by technological diversity, with different raw materials displaying widely divergent technological strategies. Whether these strategies are the result of constraints imposed by the nature of the raw materials or represent differential treatment of raw materials based on availability and quality is a question currently being pursued through several means.

Recent investigations of raw material quality (Brantingham et. al., 2000; Noll, 2000) suggest that this variable is quantifiable. D. Braun has been undertaking material sciences analyses of raw material fracture predictability, the consistency with which a particular type of stone fractures, and edge durability, i.e., the ability of an edge to resist degradation by a static or dynamic force. This will allow us to relate production mode and curation to raw material properties and transport distance for the Kanjera South assemblage. In addition to traditional technological analyses, calculation of flake edge perimeter to mass ratios will allow us to assess whether hominin reduction strategies varied in order to extract more flakes per unit volume of specific raw materials over others (Braun and Harris, 2003; McPherron and Dibble, 1999; Roth and Dibble, 1998). Ultimately these analyses may help us assess whether the Oldowan was truly a “least effort” technology (Isaac and Harris, 1997; Toth, 1985) or whether a more fine-grained appreciation of the material properties of different raw materials played into hominin technological decisions.

Raw material transport

Transport distance provides information on hominin ranging behavior. While hominins throughout the Stone Age relied on local raw materials for tool manufacture, there is an increase in the maximum transport distance in industries following the Oldowan (Isaac, 1977; Potts, 1994; Rogers et al., 1994; Schick and Toth, 1993). While it is clear that Oldowan hominins regularly transported stone, the sourcing of raw materials has rarely been accomplished, and transport is generally inferred through technological analysis.

Given the relatively low density of finds, it has been suggested that stone tool use between 2.0–2.6 Ma was expedient and perhaps only seasonally carried out (Harris and Capaldo, 1993). However, the 2.0–2.6 Ma time interval is very poorly sampled, and season of site formation cannot unequivocally be assessed for any Oldowan site. It is not clear whether the low-density scatters documented thus far represent a fundamentally different system of artifact use and transport relative to sites younger than 2.0 Ma, points on the landscape that were infrequently visited by hominins, or simple sampling bias. Recently, several 2.6 Ma excavations at Gona recovered archaeological debris in concentrations comparable to those found at sites less than 2.0 Ma (Semaw et al., 2003), though in very small excavations. The density of artifacts at Lokalalei 2C, perhaps as old as 2.3 Ma, is also relatively high (Brown and Gathogo, 2002; Roche et al., 1999). Expansion of these or similar sites may ultimately prove that the resource transport dynamics characterizing Oldowan occurrences younger than 2.0 Ma were in place from the inception of the Oldowan.

Transport distances of several kilometers were suggested for the Omo Shungura Fm archaeological sites (Merrick and Merrick, 1976), but shorter distances are also a possibility (Rogers et al., 1994). The three published KBS Member sites sampled at Koobi Fora are thought to have been several kilometers from the nearest source of raw material (Isaac, 1976; Isaac and Harris, 1978; Toth, 1997). However, this estimate is based on negative evidence: no appropriately sized stream gravels have thus far been found in the paleochannel deposits around the sites. Use of raw materials not found in local drainages at OGS-7 at Gona is indicative of transport (Semaw et al., 2003).

The heterogeneity of the geology both on and in the immediate vicinity of the Homa Peninsula (Saggerson, 1952; LeBas, 1977) is reflected by artifact assemblages at Kanjera South which have much greater raw material diversity than those from other Oldowan sites (Table 1). Extensive raw material surveys both on and off the Homa Peninsula, combined with petrological and geochemical characterization of samples collected from primary and secondary rock sources, are being used to build a lithological data base for artifact raw material sourcing. Pilot geochemical work has pinpointed the primary sources of several important nonlocal raw materials, and ultimately we hope to work out transport distances for most of the major raw materials used in artifact manufacture. Thus far it appears that a high proportion of artifacts (>20%) are made of nonlocal raw materials (not available in the Kanjera South drainages), an unusual finding, given that Oldowan sites are frequently formed on or near major raw material sources (Toth and Schick, 1986).

The most secure transport distances for the Oldowan are currently from Olduvai Gorge, Tanzania (Hay, 1976; Leakey, 1971). Lava was mainly used in the form of rounded cobbles, derived from conglomerates in alluvial fan deposits south of the gorge. The nephelinite, derived from the volcano Sadiman, was probably available within a few kilometers of the Oldowan sites. Naibor Soit, an inselberg of tabular quartzite widely used in Bed I and lower Bed II times, lies within 2–3 km of most of the archaeological occurrences (Hay, 1976). This provides one of the few truly secure transport distances for the entire Oldowan. Kelogi gneiss is a rare element in several of the larger artifact samples (e.g., DK I and FLK I L/22, also known as FLK Zinj), and was transported 8–10 km from its source near the Side Gorge (Hay, 1976). A low frequency of lava artifacts in the western Bed I lake margin zone may have been transported 15–20 km from their source (Blumenschine et al., 2003). Results from Bed I Olduvai thus demonstrate that hominins used a variety of raw materials from highly localized outcrops (Naibor Soit quartzite), relatively more widespread conglomerates (e.g., Sadiman nephelinite), and rare lithologies drawn from farther afield (Kelogi gneiss). Most artifacts were probably derived from sources within 2–3 km of a site (Hay, 1976; Potts, 1988).

Further evidence of transport comes from technological analyses of stone assemblages from Koobi Fora and Olduvai. By analyzing the range and characteristics of cores and flakes, Toth (1985, 1987, 1997) demonstrated that some materials were flaked before they were introduced to the site, some were flaked on-site, and some were removed from the site after flaking. He generated predictive models of what the characteristic flake population would be from a given set of core forms. In addition, he divided whole flakes into six technological flake categories (TFCs) based on the presence or absence of cortex (the outer, weathered surface of rock) on the striking platform, and total, partial, or no cortex on the dorsal (outer) surface of the flake. TFC I–III suggest unifacial flaking of cobbles, while TFC IV–VI result from bifacial flaking of a core. Flake populations could then be characterized as predominantly coming from primary flaking of cores on-site (high frequency of types I–III) or from transported cores that had been flaked elsewhere prior to being reduced on-site (high frequency of types IV–VI). Comparison of the expected population of flake types to those recovered in the KBS and Okote Member excavations shows that flakes from predominantly later stages of core reduction are best represented archaeologically. This was used to indicate that hominins were importing and flaking cores on-site that had been previously worked elsewhere (Schick, 1987; Toth, 1997). However, Toth (1997) noted that core size had to be taken into account when using flake-type frequency to assess transport dynamics. Larger cores are more likely to produce greater numbers of TFC IV–VI flakes, simply because larger clasts yield more flakes subsequent to cortex removal than smaller clasts do. Braun et al. (2003) followed up on this observation and demonstrated empirically that small cores yield fewer flakes following cortex removal than larger cores. Braun et al. (2003) devised a multiple regression model to predict the actual position of a flake within a reduction sequence, rather than placing a flake into a relative sequence stage as is done using TFCs. Their model was applied to a newly excavated KBS Member locality at Koobi Fora, FxJj 82 (Table 1). The flake population from this site was predominantly drawn from late in the reduction sequence, demonstrating some off-site flaking of cores prior to flaking on-site.

Technological analysis of artifacts from Olduvai Gorge, Tanzania, is also suggestive of lithic transport. Study of Bed I artifacts showed no corresponding cores for flakes of some raw materials, suggesting that cores were transported away from sites, or that the number of flakes is too low to account for the number of flake scars on some cores, suggesting off-site core reduction (Kimura, 2002; Potts, 1988).

Habitual lithic transport may extend back to the first appearance of artifacts at 2.6 Ma. As noted in the discussion of raw material selectivity, chert was transported from outside the local drainage system at Gona site OGS-7 (Semaw et al., 2003). The Hata Member of the Bouri Formation in the Middle Awash, Ethiopia, provides evidence for lithic transport at 2.5 Ma (de Heinzelin et al., 1999). The ancient lake margin zone lacked lithic raw material sources. Surface or in situ artifacts are rare, and low-density scatters of in situ fossils with cut marks and percussion damage occur without associated artifacts, suggesting that artifacts were transported away from the points of faunal utilization. By at least 2.0 Ma and perhaps at the Oldowan's inception, hominins moved lithic materials over the landscape. Artifacts, derived from multiple raw material sources, were worked at multiple points on the landscape, and were sometimes deposited in quantity at relatively restricted areas that we now designate as "sites." This suggests that the Oldowan was not simply an expedient technology: the repeated carrying of artifacts for use at different points on the landscape may reflect pressure to curate or economize, based on a current or projected need for stone (Bamforth, 1986; Binford, 1979; Braun and Harris, 2003; Odell, 1996; but see Brantingham, 2003).

MODELS OF OLDOWAN SITE FORMATION

Oldowan sites consist of artifact concentrations of varying density, sometimes with associated faunal material (Table 1). Bone weathering and object refitting studies suggest that hominins repeatedly visited certain favored locales (Bunn and Kroll, 1986; Kroll, 1994; Potts, 1988). Sites where archaeological materials are dispersed through a foot or more of sediment, or where archaeological layers are stratigraphically stacked (e.g., DK I, FLK NN I, FLK I, and FLK N I at Bed I Olduvai), are indicative of locales that remained attractive to hominins over tens to thousands of years (Kroll, 1994; Leakey, 1971; Potts, 1988). The density of archaeological material can vary dramatically from site to site (Harris and Capaldo, 1993; Plummer, 2004; Potts, 1991; Rogers et al., 1994), but the sample of sites is too sparse to confidently argue that there is a trend toward increasing size over time, especially given the paucity of work in the 2.0–2.6-Ma time interval.

Excavations tend to be small and do not reach the bounds of the archaeological concentration, and fauna is frequently not well enough preserved for detailed taphonomic and zooarchaeological analyses (Table 1; Kroll, 1994). These features of the occurrences provide some limitations on interpretation of site formation processes, and bias discussion toward the Bed I excavations of Leakey (1971), which were relatively large and recovered well-preserved concentrations of fossils and artifacts. A variety of behavioral interpretations for these accumulations have been put forth, the most influential of which are summarized here.

Home base hypothesis

Based on excavations in Bed I and lower Bed II Olduvai Gorge, Leakey (1971) recognized four categories of sites: *living floors* (dense artifact and fossil accumulations with a vertical distribution of only a few inches); *butchery or kill sites* (artifacts associated with a large mammal skeleton or the skeletons of several smaller mammals); *sites with diffused material* (i.e., a substantial vertical dispersion of archaeological material); and *stream channel sites* (cultural debris in fluvial deposits). The living floors were interpreted as the campsites of early hunter-gatherers, and her interpretation of activities at these sites was strongly influenced by the work on the Kalahari San by Lee and DeVore (1976). She envisioned small groups with enough adult males to hunt, scavenge from carnivore kills, and protect dependents from other hominin groups and carnivores. Plant food provided the bulk of the calories, with small mammals, reptiles, fish, snails, grubs, and insects supplementing the diet. Sites varied in density of cultural material, with the large accumulation of artifacts and fauna on the FLK Zinj living floor being quite exceptional. Several sites were believed to provide evidence of structures. Evidence of Oldowan hominin hunting proficiency included driving large mammals into swamps (based on the skeletons of a deinothere and an elephant associated with artifacts) and dispatching antelope with blows to the head (based on several antelope crania from FLK NI with depressed fractures).

Isaac (1976, 1978, 1983a) and Isaac and Harris (1978) concurred that the dense scatters of artifacts and fossils represented Plio-Pleistocene base camps, and subsequently used the expression "type C" or "home base" to refer to them. This home base hypothesis incorporated elements that distinguish hunter-gatherer and ape adaptations: use of a central place from which hominins dispersed and returned on a daily basis; a sexual division of labor whereby males hunted or scavenged for animal tissue and females gathered plant food resources; and delayed consumption and transport of food to the base where food-sharing and social activities took place. Food-sharing was central to this behavioral complex, and provided the selective milieu for enhanced cognition, language development, and cultural rules such as marriage systems. After articulating this hypothesis, its underlying assumptions were tested with continued fieldwork at Koobi Fora (Bunn et al., 1980; Isaac, 1981, 1984; Isaac and Harris, 1997; Kroll, 1994; Schick, 1997; Stern, 1993, 1994), comparative study with material from Olduvai Gorge (Bunn, 1986; Bunn and Kroll, 1986), and actualistic research investigating foraging opportunities for plant foods (Sept, 1986, 2001; Vincent, 1984) and scavengable carcasses (Blumenschine, 1986, 1987). Taphonomic analysis of the Bed I Olduvai collections (Potts, 1984, 1988, 1991; Potts and Shipman, 1981; Shipman, 1983, 1986) and an analysis of ethnographic butchery data, carnivore kill and den site data, and preliminary faunal information presented in Leakey (1971) by Binford (1981, 1985, 1988) provided additional critiques of the home base hypothesis.

The shift in research strategies toward testing the integrity of archaeological accumulations and proving rather than assuming a behavioral relationship between fauna and artifacts at Oldowan sites (e.g., Bunn, 1981, 1983, 1986; Oliver, 1994; Petraglia and Potts, 1994; Potts, 1983, 1988; Potts and Shipman, 1981; Schick, 1997) was a critical step in Oldowan studies. This work demonstrated that hominins and carnivores both damaged bones, but that the majority of bones at sites like FLK Zinj were transported and deposited by hominins. Though Isaac (1981, 1983a,b, 1984) reformulated the home base hypothesis, using the less emotive term "central place foraging," he and his colleagues viewed the archaeological record at Olduvai and Koobi Fora as consistent with the elements of the home base hypothesis: tool use, food transport, meat consumption on a scale allowing sharing (e.g., Bunn, 2001; Bunn and Ezzo, 1993; Bunn and Kroll, 1986), possibly a sexual division of labor associated with pair bonding, and the existence of sites where hominins would come together and food debris and discarded artifacts would accumulate (Isaac, 1981). The home base hypothesis still has proponents (e.g., Clark, 1996), and it inspired a recent variant described below (the resource defense hypothesis). Several alternatives to the home base hypothesis have been developed and are also discussed here.

Carnivore kill sites and routed foraging

Binford (1981, 1984, 1985, 1988) was an early and vociferous critic of the home base hypothesis. He argued that it was a post hoc interpretation lacking critical examination of its fundamental assumptions, such as the causal link between fossils and artifacts at Oldowan sites. Binford (1981, 1984, 1985, 1988) argued that the Oldowan artifacts and fossils needed to be "linked" through middle-range theory to modern processes relevant to the formation of the archaeological record and the traces that these processes produce. In this view, actualistic experiments and naturalistic and ethnographic observations of the modern world provide the connection between specific processes and resultant traces that can be used to interpret archaeological residues. Rather than home bases, Binford (1981) argued that many sites were carnivore kills that had been picked over by hominins, providing such meager returns (some marrow or scraps of flesh) that sharing was unlikely. There was no transport of faunal material, and hominins were unable to compete with contemporary large carnivores. He modified his view on transport somewhat in the "routed foraging model," in which hominins were recurrently drawn to fixed resources (stone outcrops, stands of trees acting as midday resting sites, and water sources) where, with relatively minor transport, carcass parts would have accumulated over time (Binford, 1984).

Stone cache hypothesis

Based on his study of Olduvai Bed I fauna and artifacts, Potts (1983, 1984, 1988, 1991, 1994) argued that stone, in the form of both artifacts and manuports, was deposited at various points in the foraging range of hominins. These "caches" became secondary sources of raw material, whether established consciously or as an unconscious by-product of hominin discard behavior (e.g., stones dropped at a carcass, underneath a recurrently visited shade tree). As debris accumulated at particular drop points, it drew hominins foraging nearby as their need for stone dictated. Carcasses obtained by either hunting or scavenging would be disarticulated and transported away from the death site to the nearest cache for processing. Computer simulation indicated that the production and use of multiple caches across a given range was more energetically efficient (considering stone and carcass transport costs) than using a single home base. This analysis of Oldowan site formation suggested that sites were used intermittently over years; carnivore competition on-site was intense; and hominin processing of fauna was often hasty and incomplete. Sites were viewed as processing areas and lithic raw material stores rather than home bases. Social activities and sleeping would likely have taken place "off site," and according to Potts (1991, 1993), no specific statements about food-sharing could be made. For Potts (1991, 1993), the key adaptation of the Oldowan was the establishment of novel transport behaviors, whereby food and stone from disparate sources were brought together and archaeological accumulations formed (the resource transport hypothesis).

Favored place hypotheses

Schick (1987); see also Schick and Toth, 1993) also proposed that large archaeological accumulations could act as secondary sources of stone raw material in her favored place hypothesis. The anticipated need for stone tools led to the habitual transport of lithic material. Over time, occasional discard of lithics at "favored places" (frequently visited rich foraging areas where hominins would consume food, rest, carry out social activities, and sleep) would lead to the passive accumulation of a local store of raw material ("de facto caches"). This would depress the need for lithic transport while foraging in the immediate area and, over time, stone and debris from multiple butchery events would form dense archaeological concentrations. This model accounts for variations in site size (depending on visitation frequency and relative lithic import-export imbalance), for the occurrence of faunal remains with artifactual damage but without associated artifacts (Bunn, 1994; de Heinzelin et al., 1999; e.g., lithics exported due to a lack of local raw material), and for the presence of stockpiles of stone greatly exceeding the need as a store of material (e.g., the lithic assemblage at FLK Zinj was likely in a rich, recurrently visited foraging area). Bunn (1991) discussed "favored places" in a similar vein to Schick (1987), as attractive, recurrently visited areas (e.g., climbable trees providing shade and shelter from carnivores), where hominins could rest, socialize, and leisurely consume transported carcass parts. In the view of Bunn (1991), plant foods were likely to have been consumed where acquired, and thus a sexual division of labor was not assumed.

Redundant use of "favored places" was also noted in nonhuman primate taxa. A group of chimpanzees in Virungu National Park, Democratic Republic of the Congo, frequently reused spots in the forest for nesting or feeding, creating nonrandom distributions of debris without food-sharing or other communal activity patterns (Sept, 1992). Baboons frequently reuse sleeping sites, as the best refuges from predators are often in short supply in savanna environments (Hamilton, 1982). These studies suggest that hominins too may have used focal points in their ranging behavior that optimized sleeping and foraging benefits.

Resource defense model

Rose and Marshall (1996) considered Oldowan hominin carnivory from the perspective of nonhuman primate behavior and the likely characteristics of the Plio-Pleistocene predator guild. They noted that primates respond to predator pressure through increased sociality, cooperative protection against predation, and cooperative defense of resources. In their view, meat from hunted and scavenged carcasses was transported to focal sites, i.e., places with fixed, defendable resources (e.g., trees, water, plant foods, or sleeping sites). Group defense allowed focal sites to be used regularly for multiple diurnal and nocturnal activities, leading to the gradual accumulation of archaeological debris. The model resembles the home base hypothesis in many ways (delayed consumption, food transport to a central place, and potentially extensive food-sharing) without the emphasis on a sexual division of labor.

Dual-unit foraging model

Oliver (1994) noted that many carnivores have altricial young and under certain conditions transport food to discrete locations for consumption. Carnivores that practice carcass transport tend to live in semiopen to open habitats with high predator densities, as did Oldowan hominins. He also noted that carcass transport to a focal spot by canids and some other carnivore taxa may have arisen through the "intersection" of two independent strategies to reduce predation risk: the transport of carcass parts away from highly competitive death sites, and the attraction of foragers to dens or secure areas where altricial offspring (sometimes with caregivers) had been left for safekeeping. He argued that early *Homo* may have responded in a similar way when moving into the predatory guild: females burdened with altricial offspring, perhaps with additional caregivers, may have foraged in core areas with refuges to reduce the energetic costs of maternal foraging and the risk of predation. Noncaregivers foraging outside the core area occasionally acquired carcass parts, which would have been transported away from death sites to refuges in the core area, and so within proximity of mothers and infants. The fitness benefits of provisioning mothers, infants, and caregivers with this high-quality food may then have established goal-directed transport of food for sharing in the hominin behavioral repertoire.

Riparian woodlands model/refuging

Based on actualistic research at the Serengeti and Ngorongoro Crater, Tanzania, Blumenschine (1986, 1987; see also Blumenschine et al., 1994; Cavallo and Blumenschine, 1989; Marean, 1989) postulated that Oldowan hominins filled a "scavenging niche" based on consuming marrow, brains, and scraps of flesh from kills abandoned by large felids during the late dry season in riparian woodlands. Foley (1987) also suggested that hominin faunal acquisition would have been predominantly a dry-season activity near perennial water sources, due to the reduction of most plant foods during this "crunch" period. Hominin theft of small antelopes cached by leopards in trees, as well as the potentially substantial residues of sabertooth felid predation of megafauna, might have provided additional woodlands-based scavenging opportunities (Marean, 1989). When yields were low and predation risks high, hominins would have transported carcass parts a short distance to stands of trees where food could be consumed in safety ("refuging;" Blumenschine, 1991; Isaac, 1983a). Active sharing would not be expected, particularly if only within-bone nutrients were being consumed. If carcass yield and processing equipment needs were high, carcass parts might have been transported to a previously visited refuge site with remaining usable stone. Food-sharing would be more likely in this scenario, but would not have been the goal of the foraging strategy (as assumed by the home base hypothesis). Recurrent visits to such a site would have led to the accumulation of artifacts and bones. Transport distances were not expected to be great in the refuge model.

Near-kill accumulations and male-display

O'Connell (1997) and O'Connell et al. (1988, 2002) pointed out that the fossil assemblages and settings of many Oldowan sites share characteristics with faunal accumulations formed near hunting blinds used by Hadza hunter-gatherers in Tanzania. The Hadza near-kill accumulations form in shaded areas near perennial water sources, contain the remains of many individual animals, include taxa from diverse habitats, and are dominated by head and limb bones. O'Connell et al. (1988, 2002) believed that Oldowan sites represent near-kill points on the landscape where scavenging and hunting opportunities were concentrated enough to allow the formation of large, taxonomically diverse assemblages over time. Their interpretation of hunter-gatherer large mammal acquisition is that males pursue it more for status than subsistence, i.e., it is a form of mating investment rather than paternal investment. They believe that Plio-Pleistocene *H. erectus* carcass acquisition was also display-driven, that large mammal carcasses were generally obtained through aggressive scavenging, and that at these encounters *H. erectus* males had the opportunity to display their mettle to other group members by threatening and trying to drive carnivores off of kills. In their view, roasted underground storage organs (USOs) obtained by female foraging and shared between grandmothers and their daughters and grandchildren were the critical dietary element in the emergence of large body and brain size in human evolution.

Table 3 provides an overview of some of the variables discussed in the models described above. The "carnivore kill site" model of Binford (1981) has largely been discarded. It was based on flawed skeletal part data (Bunn and Kroll, 1986), and carcasses ravaged to the degree described by Binford (1981) occur today in highly competitive, dangerous contexts where utilizable residues are rare (Blumenschine, 1987; Blumenschine et al., 1994). Researchers agree that lithic transport occurred, and the remaining models all postulate recurrent visitation of favored points or habitats on the landscape with some faunal transport. The redundant use of particular trees in woodlands by chimpanzees (Sept, 1992) and of trees, cliff faces, or caves by baboons in savanna (Hamilton, 1982) indicates that the distribution of valuable, fixed resources, such as water, fruiting trees and shrubs, and sleeping sites, can significantly impact primate land use (Rose and Marshall, 1996). Oldowan hominin ranging must have been similarly influenced by the distribution of food, water, and sleeping sites, but would have included additional considerations, such as the need to secure adequate supplies of stone for tool production and to minimize competitive interactions with carnivores over faunal resources. High stone discard rates may have been more likely in rich, frequently visited foraging areas where the pressure to transport stone was relaxed, either because a naturally occurring raw material source was nearby, or because recurrent hominin activity at a particular spot had already created a stone stockpile (Potts, 1984, 1988; Schick, 1987). The "magnets" drawing hominins back to a particular "favored place" vary somewhat from model to model, with a focus on attractive resources (e.g., trees for food, shade, shelter, and sleeping sites, or stone for artifact manufacture), socioeconomics (e.g., food-sharing), or a combination of both predominating. There are similarities between models: the resource defense model recalls the home base hypothesis, without assuming a sexual division of labor or pair-bonding between males and females. Transport distance was potentially longest for these two models, as they posit food transport to specific, defended points on the landscape and not simply to the nearest refuge point or cache of stone. The riparian woodlands model and male display model are similar in terms of habitat (near water woodlands) and season (dry) of site formation, and both argue for short faunal transport distances. It is likely that different models, or components of these models, could explain the formation of different Oldowan sites depending on vegetation structure, the distribution of critical fixed resources, the density and feeding adaptations of sympatric carnivores, and the particular socioeconomic structuring of the hominin group itself. As Potts (1994) argued, it is useful to assess hominin behavior from the perspective of specific key variables, rather than trying to fit archaeological data to a particular static model. A number of critical variables for assessing the socioeconomic function of Oldowan sites remain in dispute: the duration of site formation, degree of faunal transport, rank of Oldowan hominins within the predatory guild, degree of predator-pressure on hominins at archaeological sites, degree of carcass completeness and faunal acquisition strategies, and nutritional importance of meat in the diet. These points are addressed in turn below. However, a single Oldowan zooarchaeological assemblage, FLK Zinj, has dominated discussions of Oldowan hominin carnivory. The conclusions that can be drawn about hominin hunting and scavenging practices, as well as the nature of hominin-carnivore interactions, will be limited until more assemblages are analyzed with a single, consistent set of methodologies.

DURATION OF SITE FORMATION AND FREQUENCY OF CARCASS ACCESS

The interval that hominin activities were carried out on-site is critical for interpreting aspects of Old-

TABLE 3. Comparison between different models of Oldowan site formation[1]

Model	Central place foraging	Habitat of site formation	Seasonality of carcass acquisition	Mode of size 1–2 carcass acquisiiton	Mode of size 3+ carcass acquisiiton	Degree of on-site competition with carnivores
Home base hypothesis	Yes	Varied	Year-round	Mixed[2]	Probably scavenged	Low
Carnivore kill sites	No	Varied	Year-round	Passive scavenging	Passive scavenging	Not stated
Routed foraging	No	Resource/refuge areas	Year-round	Passive scavenging	Passive scavenging	Low
Stone cache	No	Varied	Year-round	Mixed	Mixed	High
Favored places	No	Resource/refuge areas	Year-round	Mixed	Not explicitly stated[3]	Low
Resource defence model	Yes	Varied; fixed resources	Year-round	Mixed	Mixed	Low
Dual-unit foraging model	No	Woodland	Year-round	Mixed	Mixed	Low
Riparian woodlands/ refuging	No	Riparian woodland	Predominantly dry season	Passive scavenging	Passive scavenging	Low
Near kill/male display	No	Riparian woodland	Predominantly dry season?	Mixed	Active scavenging	Low

Model	Degree of carcass transport	Site formation duration[7]	Nutritional importance of meat[9]	Sexual division of labor	Active sharing of meat
Home base hypothesis	Potentially long[4]	Months?	Important	Yes	Yes
Carnivore kill sites	None	Not explicitly modeled	Not important	Probably not	No
Routed foraging	Short[5]	Not explicitly modeled	Not important	Probably not	No
Stone cache	Variable[6]	5–10 years	Important	Unknown	Unknown
Favored places	Variable	Not explicitly modeled[8]	Not explicitly stated[10]	Unknown	Yes?
Resource defense model	Potentially long	Not explicitly modeled	Important	Unknown	Yes
Dual-unit foraging model	Potentially long	Not explicitly modeled	Important	No	Perhaps
Riparian woodlands/refuging	Short	Not explicitly modeled	Not important	Unknown	No
Near kill/male display	Short	Not explicitly modeled	Not important	No	Yes

[1] Mammal size classes follow Brain (1981) and Bunn (1986) as follows: size 1, 23 kg or less; size 2, 23–114 kg; size 3, 114–341 kg; size 4, 341–909 kg; size 5, >909 kg.

[2] Mixed refers to a combination of hunting and scavenging or both active and passive scavenging.

[3] Schick (1987) was not explicit; Bunn (1991) argued for a mixed acquisition strategy.

[4] Unstated but potentially more than a kilometer (O'Connell et al., 2002).

[5] Several hundred meters or less (O'Connell et al., 2002).

[6] Dependent on cache density on landscape.

[7] Refers to estimated duration of site formation prior to burial of thin (<10 cm) archaeological horizons such as DK I level 3.

[8] Not modeled by Schick (1987).

[9] Refers to organs, muscle tissue, and within-bone nutrients, including marrow and brain tissue.

[10] Not stated by Schick (1987).

owan hominin behavior, including estimating the frequency of access to carcasses. If hominins had early access to and thoroughly processed a large number of carcasses over a short period of time, it would suggest that animal tissue was an important part of their diet and that their rank relative to contemporary carnivores was at least moderately high. Multiple, discrete layers of archaeological material through a sequence may represent discontinuous, repeated use of particular spots on the landscape by hominins over time (Kroll, 1994). Sites where artifacts and archaeological fauna were diffusely distributed through fine-grained sediments may represent archaeological materials disturbed by biogenic or mechanical processes (e.g., trampling, termite activity). Inferring the frequency of carcass acquisition is best pursued with thin archaeological levels where debris was accumulated on a single land surface, and burial was probably rapid. Three Oldowan archaeological site levels (DK I level 3, FLK NN I level 3, and FLK I level 22, also known as FLK Zinj) within the Bed I Olduvai Gorge sequence were only 9 cm (3.5 inches) thick and likely fit these criteria (Bunn and Kroll, 1986, 1987; Potts, 1986, 1987, 1988).

The amount of time represented by ESA archaeological layers has often been estimated using average sedimentation rates (Kappelman, 1984; Stern, 1993) and bone-weathering stages (Bunn and Kroll, 1986; Lyman and Fox, 1989; Potts, 1986). Average sedimentation rates are only accurate if deposition was constant and uniform over the period of time sampled, which is rarely the case in a terrestrial environment. Much of the time in a terrestrial sequence is "nondepositional time," in that sediments are either not laid down or they are laid down but eventually remobilized by water or wind action and redeposited elsewhere (Leeder, 1982). An average sedimentation rate generated from a long terrestrial stratigraphic sequence is going to have this "nondepositional time” built into it and is going to vastly overestimate the amount of time represented by a thin archaeological level. For example, a mean sedimentation rate for the Bed I Olduvai lake margin deposits provided an estimate of approximately 1,500 years for burial of the FLK Zinj assemblage (Kappelman, 1984). In contrast, Schick (1986; see also Schick and Toth, 1993) established simulated sites of replicated artifacts and modern animal bones in fluvial and lacustrine settings analogous to where Oldowan sites were formed in the past. Many of the simulated sites were buried during her 4-year study period, indicating that some Oldowan debris concentrations were likely sealed very rapidly.

The strongest evidence for rapid burial is provided by the fossils themselves. The larger bones and artifacts from DK I level 3, FLK NN I level 3, and FLK Zinj were as thick as their respective layers, indicating to both Potts (1986, 1987, 1988) and Bunn and Kroll (1986, 1987) that deposition was on a single stable land surface. Bone surfaces crack and peel progressively when exposed to the elements on a landscape. These changes were defined as six weathering stages, each with an associated rate (Behrensmeyer, 1978; Lyman and Fox, 1989). Bunn and Kroll (1986) argued that the subaerial weathering features of the bones from FLK Zinj reflect burial time at the site, and using the weathering stage criteria of Behrensmeyer (1978), they argued that all of the bones could have been deposited by hominins over a short period of time, followed by burial over several years. Potts (1986, 1988) interpreted the subaerial weathering stages of long bone shafts from these levels to estimate the length of time over which bones were exposed to the elements, rather than burial time. He estimated that hominin activities were carried out on-site for 5–10 years prior to burial. Though they disagree on what bone weathering was measuring, both analyses concur that these assemblages were formed and buried in relatively short periods of time (10 years or less). A short period of deposition is consistent with pristine fossil preservation, the presence of complete bones or large bone fragments spanning the thickness of the sedimentary unit likely to have been fragmented if exposed for decades or longer, and the fact that bones on modern land surfaces rarely survive more than 15 years (Behrensmeyer, 1978). DK I level 3, FLKNN I level 3, and FLK Zinj yielded a minimum number of 37, 34, and 36 macromammal individuals, respectively (Potts, 1984). The excavations by Leakey (1971) did not fully expose these archaeological concentrations, so these minimum numbers of individual (MNI) values likely underestimate the number of carcasses accumulated on-site. Moreover, extensive analysis of limb shafts by Bunn and Kroll (1986) provided a higher estimate of the minimum number of limb elements (MNE) and MNI for the FLK Zinj assemblage (MNI = 48). Given that a group of Oldowan hominins is likely to have formed accumulations at multiple sites across the landscape, and that meaty carcasses were frequently acquired at FLK Zinj (see below), the high acquisition rates implied here strongly suggest that animal tissue was a frequent and important component of the diet of the Bed I hominins.

FAUNAL TRANSPORT DISTANCE

As seen in carnivores, the transport of carcass parts by Oldowan hominins was most likely an antipredator strategy to limit competition at death sites (Oliver, 1994). Isaac (1978) and Rose and Marshall (1996) argued that the size, taxonomic diversity, and habitat preferences of the animals found in Oldowan assemblages suggest that hominins were transporting carcasses from multiple habitats to a central location. Though not specified, the implication is that transport distances frequently reached a kilometer or more. In the routed foraging, refuge, and near-kill/male display models of site formation, the assumption is that faunal transport was limited to several hundred meters (O’Connell, 1997). Carcass encounter rates and transport decisions vary with prey body size (Bunn et al., 1988; O’Connell et al., 1990). FLK Zinj may be an outlier in terms of assemblage size, but it is the Oldowan accumulation that has been most discussed in the literature. The faunal assemblage is composed of approximately 46,000 bones (excluding microfauna), representing an MNI of between 36 (Potts, 1988) and 48 (Bunn and Kroll, 1986) individual animals from at least 16 taxa. Of relevance here is the expected transport distance for size 3 and 4 (Brain, 1981; wildebeest- to Grevy’s zebra-sized) mammals, of which there was an MNI of between 22 (Potts, 1988) and 31 (Bunn and Kroll, 1986) at the site. In general, size 3–5 (Brain, 1981; Bunn, 1986) mammals are thought to have been scavenged (Blumenschine, 1995; Bunn and Ezzo, 1993; Potts, 1988).

O’Connell et al. (2002) noted that Hadza hunter-gatherers armed with bows and hunting from blinds can form large, taxonomically diverse bone assemblages without long-distance transport. The taxonomic diversity of the assemblage is a reflection of the arid climate the Hadza live in, with the intensity of the dry season forcing animals with a variety of habitat preferences to range through riparian woodlands to reach perennial water sources. Annual precipitation was higher and the degree of seasonality likely much lower during most of Bed I Olduvai deposition (Cerling and Hay, 1986; Fernandez-Jalvo et al., 1998), and in wetter savannas today there is less dry-season movement of fauna through riparian woodlands (Tappen, 1995). Moreover, hunting from blinds with projectile weapons is not an appropriate analog for the frequency and spatial focus of scavenging opportunities provided by large carnivores, which is likely what Oldowan hominin medium-sized carcass acquisition depended on. The degree of kill concentration necessary to account for the MNI at the Olduvai levels mentioned above has not been observed in studies of large predators or in landscape taphonomic studies in modern savannas (Behrensmeyer et al., 1979; Behrensmeyer and Dechant Boaz, 1980; Blumenschine, 1986; Domínguez-Rodrigo, 2002; Foley, 1987; Hill, 1975; Kruuk, 1972; Potts, 1988; Schaller, 1972; Tappen, 1995, 2001). Carnivores would have to have killed approximately 25 size 3–4 mammals within a few hundred meters of the FLK Zinj locale, and hominins to have acquired every carcass, over a period of no more than 10 years (Potts, 1988) for the medium-sized mammal component of the Zinj assemblage to have formed through short-distance transport. In the rare occurrences where catastrophic mortality concentrates carcasses in one place or carnivores make a mass kill, prey taxonomic diversity is low (Capaldo and Peters, 1995; Kruuk, 1972; Schaller, 1972). Hence the size and taxonomic diversity of the FLK Zinj assemblage (and based on high MNI values, other Bed I site levels; Potts, 1988) are suggestive of transport beyond that predicted by the refuge or near-kill models. Given that stone deposited at Bed I sites was often transported several kilometers from its source, the transport of fauna for a kilometer or more may not be unreasonable.

HOMININ-CARNIVORE INTERACTIONS

Hominin rank in the predatory guild

Cut marks and percussion damage on bones indicate that hominins encroached on the predatory guild from the inception of the Oldowan (de Heinzelin et al., 1999; Semaw et al., 2003). Today, the guild of African large carnivores is highly competitive, as it likely was in the past (Brantingham, 1998a; Caro and Stoner, 2003; Lewis, 1997; Van Valkenburgh, 2001). Interspecific competition for possession of kills is common, as is intraguild predation (often without consumption) on both juvenile and adult competitors. Body size generally determines rank within the guild (e.g., lion > hyena > wild dog), but grouping behavior can overturn this rule (e.g., a large group of hyenas can displace a small pride of lions from a kill).

The late Pliocene guilds of large predators in East and South Africa were probably twice as large as the modern predatory guilds in those regions today (Lewis, 1997; Pobiner and Blumenschine, 2003; Turner, 1990; Van Valkenburgh, 2001; Walker, 1984) (Table 4). The fossil guilds contained a greater number of felids and hyenids, distributed in both open and more wooded settings. The greater diversity of carnivores relative to modern ecosystems might indicate that competitive interactions occurred more frequently in the past (Lewis, 1997; Van Valkenburgh, 2001). However, increased predator taxonomic diversity was matched by a greater diversity of potential prey, suggesting a greater degree of niche partitioning in the large herbivore and carnivore guilds than is seen in Africa today (Blumenschine, 1987; Lewis, 1997). Moreover, it should not be assumed that the taxa listed in Table 4 were sympatric, as this list was drawn from a number of time-averaged, potentially habitat-transgressive fossil assemblages (Walker, 1984), and high-ranking carnivore taxa may have locally limited or excluded those of lower rank (e.g., lions and hyenas in the modern guild can limit the distribution of wild dogs; Creel and Creel, 2002).

The number of scavenging opportunities, passive and confrontational, available to Oldowan hominins in a particular locale would have been dependent on the local density, degree of sociality, and feeding specializations of the carnivores there (Blumenschine, 1987; Lewis, 1997; Turner, 1990; Van Valkenburgh, 2001). For example, defleshed carcasses providing within-bone nutrients may have been more common in areas where felids predominated vs. those with high densities of hyenids and/or canids. Van Valkenburgh (2001) argued that carnivore densities were likely much higher in the Plio-Pleistocene, because human persecution has lowered carnivore densities in modern analog game reserves where density calculations are made. If true, competitive interactions over carcasses could have been very high in the past.

Our understanding of carnivore-hominin competition is hampered by the paucity of carnivore remains at any particular locality and the limitations in our knowledge of carnivore paleobiology. However, some conclusions can be drawn from modern carnivore guild dynamics and from the taphonomic assessment of Oldowan zooarchaeological samples. At approximately 35 kg (Tables 2 and 4), *H. habilis* sensu stricto would have been smaller than 8 of 12 large carnivore taxa known from fossil sites in East Africa. Given that body size often predicts rank in the carnivore guild, an individual *H. habilis* would likely not have fared well in a contest with many of its contemporary carnivores. Competition with large carnivores may have favored cohesive groups and coordinated group movements in *H. habilis*, cooperative behavior including group defense, diurnal foraging (as many large predators preferentially hunt at night) with both hunting and scavenging being practiced as opportunities arose, and the ability (using stone tools) to rapidly dismember large carcasses so as to minimize time spent at death sites (Foley, 1987; Oliver, 1994; Rose and Marshall, 1996; Van Valkenburgh, 2001). This view of hominin foraging ecology and sociality may ultimately be testable, if zooarchaeological assemblages likely to have been formed by *H. habilis* provide evidence of consistent, early access to carcasses at a relatively high frequency. This would suggest that a group of *H. habilis* individuals was able to modify the "body size = rank" rule of carnivore guild hierarchy, and so, under certain contexts at least, was able to actively compete with large carnivores. Alternatively, evidence for consistent late access to carcasses would indicate that *H. habilis* was a low-ranked member of the Plio-Pleistocene carnivore guild and would provide few inferences on group cohesiveness and the likelihood of extensive sharing. *H. habilis* is the sole member of the genus *Homo* known from Bed I Olduvai (Tobias, 1991a,b), and sites such as FLK Zinj (see below) may ultimately be confidently attributed to this taxon.

H. erectus was equivalent in size to, or larger than, all but four carnivores, and two of these four (*Homotherium* and *Megantereon*) may have been extinct by 1.5 Ma (Werdelin and Lewis, 2001). Larger body size would have enhanced its competitive ability within the predatory guild, and perhaps not surprisingly Developed Oldowan and Acheulean archaeological residues attributable to *H. erectus* document extensive use of open habitats, early access to fauna, and possibly the ability to exclude carnivores from points on the landscape (Bunn et al., 1980; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo et al., 2002; Monahan, 1996; Potts, 1989, 1994; Potts et al., 1999). Ongoing work at Olorgesailie, Kenya (Potts et al., 1999), and Peninj, Tanzania (Domínguez-Rodrigo et al., 2002), promises to greatly improve our understanding of the behavioral ecology of this taxon.

On-site competition with carnivores

Evidence for the competitive ability of Oldowan hominins may be assessed through careful taphonomic analysis of zooarchaeological samples. Potts (1984, 1988, 1996b) used several lines of evidence to argue that carnivores limited hominin on-site activities at Bed I Olduvai. Carnivore tooth marks occur on bones from each of the archaeological levels he analyzed, and some bones exhibit damage attributable to a large, bone-crunching carnivore like the modern spotted hyena (*Crocuta crocuta*). Small, immature carnivore remains are relatively common, potentially reflecting individuals killed in on-site competition (hominin vs. carnivore and/or carnivore vs. carnivore) for animal tissue. Complete long bones lacking tool marks are not uncommon, and may indicate hasty hominin faunal processing and the abandonment by hominins of resources attractive to carnivores.

Researchers generally agree that Bed I zooarchaeological assemblages show extensive carnivore damage. But measures of the intensity of bone damage at FLK Zinj suggest that carnivore ravaging was *extensive* but not *intensive* (Blumenschine, 1995; Blumenschine and Marean, 1993; Bunn and Kroll, 1986; Capaldo, 1997; Oliver, 1994). A wide range of skeletal parts shows cut marks, and hammer-stone processing was pervasive and thorough (for an alternate view, see Potts, 1987, 1988). Very little long bone fragmentation is attributable to carnivore activity (Oliver, 1994). The representation of greasy bones attractive to carnivores (axial elements, scapulae, and long bone epiphyses) is high relative to controlled spotted hyena feeding experiments (see below), suggesting that on-site competition for skeletal elements was not intense at FLK Zinj and some other Oldowan occurrences (Blumenschine and Marean, 1993; Capaldo, 1997; Marean and Spencer, 1991; Marean et al., 1992; O' Connell et al., 2002). Finally, the complete long bones noted above may have been abandoned by hominins satiated with flesh. Their survival on-site is further indication of a low-competition context, as few bones would have escaped damage if on-site competition was intense (Capaldo, 1997; Domínguez-Rodrigo, 2002; see below).

TABLE 4. Composite species list of large (>20 kg) mammalian carnivores known from the Plio-Pleistocene of East Africa[1]

Species	Description	Estimated body mass (kg)
Felidae		
Homotherium crenatidens	Sabertooth cat	170
Panthera leo	Lion	170
Dinofelis aronoki	"False" sabertooth cat	150
Megantereon cultridens	Sabertooth cat	95
Panthera pardus	Leopard	65
Acinonyx jubatus	Cheetah	55
Canidae		
Canis **sp.**	Wolf-like canid	30
Hyaenidae		
Crocuta ultra	Ancestral spotted hyena	50
Hyaena brunnea	Brown hyena	39
Hyaena hyaena	Striped hyena	32
Chasmoporthetes nitidula	Cursorial hyena	21

[1] Minimum list, as two incompletely resolved *Panthera* spp. were not included. Extinct taxa in bold. After Van Valkenburgh (2001), Table 5.3, p. 110).

OLDOWAN HOMININ CARNIVORY

If Oldowan hominins were, at least in some ecosystems, getting fairly regular access to carcasses, how complete were they and how were they acquired? How distinctive was Oldowan hominin carnivory relative to meat-eating in living nonhuman primates?

Prey selectivity

Several lines of evidence suggest that small mammal hunting was common within the Homininae. Primate hunting, per se, is not unusual. The fact that vertebrates are hunted by a diverse array of primate taxa (9 families, 26 genera, and 38 species, according to Butynski, 1982) indicates that hominin hunting is not an unreasonable proposition. A strong argument can be made that hunting is a homologous behavior in chimpanzees and humans (McGrew, 1992; Wrangham et al., 1994; Wrangham and Peterson, 1996). If this is the case, small mammal hunting was likely to have been conducted by a variety of hominin taxa. Studies of chimpanzee hunting are useful in considering australopithecine predatory behavior by indicating the prey characteristics of a large-bodied primate hunting and processing fauna without the benefits of a lithic technology (Plummer and Stanford, 2000; Stanford, 1996). With this in mind, foraging for animal tissue by chimpanzees can be usefully contrasted with Oldowan hominin carnivory, to exemplify its departure from the putative ancestral condition.

All nonhuman primates are limited to relatively small, frequently immature prey, which can be easily captured, dispatched, disarticulated, and consumed (Strum, 1981; Stanford, 1996; Rose, 1997; Uehara, 1997). Table 5 compares the faunal characteristics of Bed I Oldowan assemblages with chimpanzee and baboon prey (e.g., Boesch and Boesch, 1989; Mitani and Watts, 1999; Stanford, 1996; Uehara, 1997; Strum and Mitchell, 1987; Hausfater, 1976). Here, "faunal resource" refers to remains acquired through either hunting or scavenging. Chimpanzees hunt a variety of taxa (from 6–17 species, including rodents), but red colobus make up no less than 53% of the total prey sample. In contrast, between 8–24 macromammalian taxa (mammals larger than 2 kg in size) were present at each of the Oldowan sites. Moreover, the most common species at the hominin sites made up a smaller proportion (between 10–40%) of the total assemblage than the most common taxon consumed by chimpanzee communities or baboon troops. Chimpanzees hunt small prey, falling within the "very small" size class (2–10 kg) of Potts (1988) and within or below size 1 (23 kg or less) of Brain (1981). While a wide size range of taxa were apparently processed (Table 6), the most commonly represented remains at the Olduvai sites fall in the medium size class of Potts (1988; 72–320 kg; roughly equivalent to size 3 of Brain, 1981) far larger than chimpanzee prey (see also Bunn, 1986; Bunn and Kroll, 1986). Bed I hominin assemblages contain a higher percentage of adult individuals of all species, compared to the greater percentage of immature individuals consumed by chimpanzees (Table 5). Finally, differences exist between the habitat preferences of taxa utilized by chimpanzees vs. those utilized by hominins. The habitat preferences of utilized species provide an indirect way to assess the foraging ecology of a predator (Foley, 1987; Plummer and Bishop, 1994). Chimpanzee prey are all derived from forest and woodland settings, and thus reflect their preferred habitats. Baboons, which commonly utilize more open habitats than chimpanzees, consume prey with woodland, bushland, and open grassland habitat preferences. Similarly, fauna deposited at Bed I hominin sites come from a broad spectrum of habitats, minimally from dense woodland to open grassland (Kappelman, 1984; Potts, 1988; Plummer and Bishop, 1994; Kappelman et al., 1997; Fernandez-Jalvo et al., 1998).

The data presented in Table 5 demonstrate that, with regard to the use of fauna, Bed I Oldowan hominin foraging ecology was significantly more generalized than that practiced by chimpanzees. Oldowan hominins recognized a greater variety of taxa as resources, across a wider spectrum of body sizes and from a greater variety of habitats. They were able to obtain tissue from adult as well as juvenile prey. In terms of modal prey size, percentage of immature prey individuals, and habitat preferences of prey taxa, the Bed I assemblages accumulated by hominins seem quite similar to roughly coeval assemblages formed by large carnivores (Table 5). These contrasts between chimpanzee and Oldowan hominin faunal utilization almost certainly reflect a crucial difference in their foraging behavior: Oldowan hominins likely acquired carcasses through scavenging as well as hunting. The scavenging of large mammal carcasses by Oldowan hominins is a clear departure from the use of vertebrate tissue by nonhuman primates. Scavenging is extremely uncommon, and in chimpanzees, baboons, and capuchins largely consists of pirating freshly killed prey from other group members. Chimpanzees have also pirated fresh kills made by baboons (Morris and Goodall, 1977). Both baboons and chimpanzees are reluctant to scavenge tissue from animals they have not killed or not seen killed (Strum, 1983; Hasegawa et al., 1983; Muller et al., 1995). This reluctance may have an evolutionary basis. Unlike large mammalian carnivores that routinely scavenge, primates do not have physiological mechanisms to deal with diseases directly transferable from carcass to consumer (Ragir, 2000; Hamilton and Busse, 1978). Therefore, an aversion to carrion is probably adaptive, as a means to avoid disease from tainted meat and/or to avoid predators drawn to large mammal carcasses (Hamilton and Busse, 1978; Strum, 1983; Nishida, 1994). While the inhibition against scavenging is strong, it can be overridden in the appropriate social context. Strum (1983) found that social cues were important in determining the suitability of a carcass not previously encountered by some members of a baboon group. A carcass was viewed as an attractive food item by initially reluctant individuals once one group member began to feed on it. The importance of local social context at least partially explains differences in prey selectivity, prey age, and the propensity to scavenge among different chimpanzee communities (Table 5) (Uehara, 1997).

The contrast between Mahale and Tai is particularly illuminating: Mahale chimpanzees hunt nearly three times as many mammalian species (including ungulates ignored at Tai), take more immature individuals, and, unique among chimpanzee communities, have on rare occasions scavenged animals they had not seen killed (Hasegawa et al., 1983; Nishida, 1994). Their scavenging includes feeding on an adult bushbuck cached in a tree by a leopard. This episode is particularly intriguing, in that chimpanzees were utilizing a kill well out of the size range of their hunted prey (adult bushbucks weigh 24–80 kg; Kingdon, 1997). Differences in prey characteristics and scavenging behavior may, like the use of hammers-and-anvils for nut-cracking among some West African chimpanzee populations, reflect the development of community-specific behavioral

TABLE 5. Comparison of mammalian faunal resources utilized by representative chimpanzee communities and Oldowan hominids[1]

Locality	Number of species utilized	Most common species	Modal size	% immature (all species)	Transport of faunal resources	Scavenge fauna	Habitat preferences of utilized fauna
Pan troglodytes							
Gombe, Tanzania	8	82% (*C. badius*)	1 kg (for *C. badius*)	89%	No	No	Woodland
Ngogo, Uganda	7	91% (*C. badius*)		79%[2]	No	No	Rain forest
Mahale, Tanzania	17	53% (*C. badius*) in 1981–1990; 82% (*C. badius*) in 1991–1994	5 kg (for *C. badius*)	76%	No	Rare	Forest and woodland
Tai, Ivory Coast	6	78% (*C. badius*)	5 kg (for *C. badius*)	56%	No	No	Rain forest
Papio anubis							
PHG (1973–1977)	6	53% (*L. capensis*)	<3.5 kg	High	No	No	Bushland and grassland
PHG (1970–1971)	5	42% (*G. thomsoni*)	<3.5 kg	High	No	No	Bushland and grassland
Papio cynocephalus							
Amboseli	7	47% (*L. capensis*)	<3.5 kg	High	No	No	Acacia woodland and grassland
Bed I Olduvai, hominid sites							
FLK N L/6	12	17% (both *K. limnetes* and *E. oldowayenis*)	72–320 kg	35%	Yes	Yes	Woodland to grassland
FLK “Zinj”	14	23% (*A. recki*)	72–320 kg	28%	Yes	Yes	Woodland to grassland
FLK NN L/3	8	40% (*K. sigmoidalis*)	72–320 kg	47%	Yes	Yes	Woodland to grassland
DK L/2	24	10% (both *A. recki* and *P. altidens*)	72–320 kg	29%	Yes	Yes	Woodland to grassland
DK L/3	20	12% (*A. recki*)	72–320 kg	32%	Yes	Yes	Woodland to grassland
Bed I Olduvai, carnivore sites							
Long K	6	38% (*P. altidens*)	72–320 kg	21%	Yes	Yes	Woodland to grassland
FLK NN L/2	8	29% (*K. sigmoidalis*)	72–320 kg	35%	Yes	Yes	Woodland to grassland

[1] Micromammal, carnivore, and hominin taxa were not included in counts of species utilized at Olduvai, as these may not reflect hominin subsistence activities (e.g., micromammals were largely introduced by raptors and/or mammalian carnivores; (Fernandez-Jalvo et al., 1998). Olduvai data calculated from MNI values in Potts (1988). Chimpanzee data from Boesch and Boesch (1989), Boesch and Boesch-Achermann (2000), Mitani and Watts (1999), Stanford (1996), and Uehara (1997). Baboon data from Strum and Mitchell (1987) and Hausfater (1976). *C. badius = Colobus badius, L. capensis = Lepus capensis, G. thomsoni = Gazella thomsoni, K. limnetes = Kolpochoerus limnetes, E. oldowayenis = Equus oldowayensis*, A. recki = *Antidorcas recki, K. sigmoidalis = Kobus sigmoidalis, P. altidens = Parmularius altidens.*

[2] *C. badius*, only.

traditions (McGrew, 1992; Tomasello, 1994; Uehara, 1997). It also implies that community-specific behavioral traditions in faunal use or lithic technology may have existed in the Oldowan, but are thus far not apparent due to the coarseness of the archaeological record.

The inhibition against scavenging in all nonhuman primates contrasts strongly with the broad occurrence of hunting in the order (Butynski, 1982). Given the low risk involved in small mammal hunting and the potential health and predation risks associated with scavenging, it seems likely that a scavenging tradition would have developed in hominin communities that already hunted small mammals, and valued vertebrate tissue. The expansion of the diet to include scavenged fauna is best considered in light of the changing plant food resource base available to hominins during the late Pliocene, as discussed above in terms of paleoecology and when considering the onset of the Oldowan, below.

Carcass completeness and faunal acquisition strategies

Because resource availability depends on the timing of access, some researchers have relied on the relative frequency of body part representation (skeletal part profiles) to assess whether hominins had access to complete animal carcasses (Blumenschine, 1995; Bunn, 2001; Bunn and Kroll, 1986; Capaldo, 1997; Domínguez-Rodrigo, 1997, 2001; Lupo and O’Connell, 2002; O’Connell et al., 2002; Oliver, 1994; Potts, 1988; Selvaggio, 1998). Early access, either through confrontational scavenging (driving carnivores off a nearly complete or complete kill) or hunting, provides most or all of a carcass. Late access through passive scavenging provides a smaller selection of carcass parts, often limited to within-bone nutrients (marrow and/or brains; Binford, 1981; Blumenschine, 1986). Oldowan faunal assemblages from Olduvai Gorge are frequently dominated by meat-bearing limb bones and skull fragments. This

TABLE 6. Preliminary size class attributions of the pooled Excavation 1 samples[1]

Mammal size class	Excavation 1 NISP	Excavation 1 percent	Bed I average
Small (2–72 kg)	520	39%	20%
Small/medium boundary	208	16%	
Medium (72–320 kg)	593	44%	55%
Large and very large (>320 kg)	12	1%	25%
Total	1,333	100%	100%

[1] Size class definitions and averages for five Oldowan assemblages from Bed I Olduvai from Potts (1988). Note that Kanjera tallies do not yet include bones from spit bags or sieving; these are likely to further increase the proportion of small taxa.

finding was used to argue that hominins had early access to relatively complete carcasses and were disarticulating limbs and skulls for transport from death sites, thereby reducing transport costs and maximizing the utility of transported remains (Bunn and Kroll, 1986; Bunn et al., 1988). However, it is now clear that the action of large carnivores, particularly spotted hyenas, can lead to a "limb-and-head-dominated" skeletal assemblage, even if axial bones were initially present. In experiments in natural and captive settings, spotted hyenas presented with a range of skeletal elements preferentially consumed grease-rich vertebrae and ribs, with innominates, scapulae, and foot bones also being differentially consumed in some experiments (Capaldo, 1997, 1998; Marean et al., 1992). The carcass transport decisions made by modern hunter-gatherers also do not neatly fit a "limb and head" transport model (Monahan, 1998; O'Connell et al., 1990; Oliver, 1993; Yellen, 1977). Moreover, hunter-gatherer cooking practices (particularly boiling bones in pots to extract grease and adhering meat scraps) provide a transport influence that would not have existed in the remote past. Some researchers continue to rely on skeletal part frequencies to assess the timing of hominin access to carcasses (e.g., Brantingham, 1998a,b), but the issue of equifinality (multiple pathways to the same end result) argues that skeletal part data alone should not be used for this task.

The timing and agents involved in carcass utilization can also be studied through bone surface damage (Binford et al., 1988; Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Bunn, 2001; Capaldo, 1997, 1998; Domínguez-Rodrigo, 1997, 1999a, 2001, 2002; Lupo and O'Connell, 2002; Marean and Spencer, 1991; Marean et al., 1992; Oliver, 1994; Selvaggio, 1994, 1998). Carnivores and tool-wielding hominins process carcasses in different ways. Carnivores strip meat off bones (leaving tooth marks), gnaw on bone ends (epiphyses) to access blood and grease, and, if the epiphyses are destroyed, attack shaft cylinders from the ends to access the fatty marrow (Brain, 1981). Large cats such as lions (*Panthera leo*) can crack bones from size 2 (impala-sized) and smaller prey, but are limited to the viscera and flesh of size 3 (wildebeest-sized) and larger taxa (Blumenschine, 1987). Spotted hyenas have specialized jaw and tooth morphology and are exceptional among living carnivores in their ability to completely consume edible tissue of size 3 mammal, including breaking long bone shafts to access marrow (Brain, 1981; Lewis, 1997).

Oldowan hominins lacked the meat-shearing and bone-crunching abilities of carnivores, but could carry out the same functions with their simple stone toolkit (Schick and Toth, 1993). Sharp stone flakes were used to slice off meat and disarticulate carcass parts, sometimes leaving cut marks. Within-bone nutrients were accessed by placing bones on an anvil and striking them with a hammer stone. Resultant percussion marks include microstriations or pits and grooves containing microstriations (Blumenschine and Selvaggio, 1988; Selvaggio, 1994), as well as distinctive load point and fracture surface morphology (Oliver, 1994; Plummer, personal observations). Thus, bone surface damage can inform on the agents involved in bone modification and perhaps the timing of carnivore and hominin access, if a dominant sequence of access held throughout the formation of an assemblage.

Blumenschine (1988, 1995), Capaldo (1997, 1998), and Selvaggio (1994, 1998) used experimental simulations in several modern Serengeti and Ngorongoro habitats to determine criteria sensitive to the timing of hominin and carnivore access to a set of bones. Several different actors were presented the same sets of bones, in an attempt to mimic the "dual patterning" of hominin and carnivore damage to Oldowan archaeological bone. Bones from size 2 and size 3 mammals were exposed first to carnivores (usually spotted hyenas) in some experiments and to "hominins" (the researchers processing defleshed carcasses for marrow) in others. In the whole-bone to carnivore models by Capaldo (1997, 1998), bones were defleshed with tools but presented whole to carnivores (spotted hyenas) for consumption. Selvaggio (1998) presented a three-stage simulation, in which carnivore access to the assemblage preceded and followed hominin marrow-processing of bones. This body of work (in concert with captive spotted hyena feeding experiments; Blumenschine and Marean, 1993; Marean and Spencer, 1991; Marean et al., 1992) suggested to these researchers that there are reliable signatures of access to carcass parts. There were extensive tooth marks on long bones (including 82.6% of midshafts) when large carnivores (spotted hyenas and lions) had first access to a fleshed carcass. Midshaft tooth-mark frequencies were depressed with hominin first access (10.5% in Blumenschine, 1988, 1995; 15.4% in Capaldo, 1997, 1998), because meat and marrow removal made bone shafts less attractive. In the whole bone to carnivore models, 57.4% of midshaft fragments were tooth-marked, reflecting spotted hyena interest in grease and marrow. Spotted hyenas frequently consumed long bone epiphyses and axial elements when scavenging hammer stone-processed bones. When these experimental results were applied to the large FLK Zinj assemblage, three researchers (Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998) suggested that the moderately high midshaft tooth-mark frequencies (57.9%), percentage of percussion marks, and deletion of long bone epiphyses were consistent with a three-stage access sequence of large felids defleshing carcasses, hominins removing remnant flesh and marrow-processing bones, and hyenas scavenging epiphyses.

Cut-mark data have been interpreted in several ways. Bunn (1986, 2001) suggested that cut-mark distribution on limbs from FLK Zinj was similar to that produced by the Hadza, clustering around areas of strong muscle attachments. This suggests that large muscle masses were stripped and consumed by Oldowan hominins. Oliver (1994) produced similar cut-mark frequency estimates, and noted that, at least for small mammals and the forelimbs of medium- to large-sized mammals, cut marks were preferentially placed on upper (meat-bearing) elements. But the lack of an experimental framework relating cut-mark frequency and distribution to flesh yield led some to suggest that the cut marks at FLK Zinj reflect hominin removal of meat scraps surviving carnivore consumption, i.e., that the cut-mark data could still be accommodated within a passive scavenging framework (Binford, 1981; Blumenschine, 1991, 1995; Capaldo, 1997; Selvaggio, 1998).

Domínguez-Rodrigo (1997, 1999b, 2002) analyzed cut-mark data from experimental studies of carcasses with varying amounts of flesh (hominin first access vs. hominin scavenging of carcasses partially or completely stripped of meat by lions) to establish a referential model for interpreting hominin meat-processing. He argued that a strong relationship exists between the amount of meat present and cut-mark representation, with upper limb elements (humeri and femora) exhibiting the highest cut-mark frequencies from defleshing. Carcasses consumed by lions in woodland settings were completely defleshed, leaving few scraps of meat for a scavenging hominin. Applying this referential framework to FLK Zinj, he argued that hominins were stripping substantial amounts of meat from carcasses in addition to marrow-processing, rather than only accessing within-bone nutrients from defleshed felid kills.

In addition to analyzing bone surface damage, Oliver (1994) assessed load points and associated fracture surfaces to determine the roles carnivores and hominins played in fracturing long bones at FLK Zinj. Though carnivore tooth marking was common, breakage attributable to carnivore activity was not. This suggested to him that a large, bone-crunching carnivore like the spotted hyena was not a primary modifier of the FLK Zinj assemblage. Cut marks were focused on meat-bearing bones, and hammer stone-induced fracturing of bones was common and thorough, and likely destroyed some epiphyses. Carnivore tooth marking was evenly distributed across meat-bearing and nonmeat-bearing bones, suggesting that gnawing was unrelated to meat removal. Oliver (1994) interpreted this overall pattern as reflecting early carcass access with subsequent defleshing and marrow-processing by hominins. Small carnivores scavenged flesh scraps, but were unable to crack bones from the hominin residues. Oliver (1994) also stated that some tooth marks might be from the hominins themselves, and not from carnivores.

In summary, all researchers agree that bones at FLK Zinj were predominantly if not exclusively transported there by hominins, and that damage implicates both carnivores and hominins in nutrient extraction. Extensive hominin marrow-processing of limb bones is also generally accepted, as is scavenging of hominin refuse by carnivores. The major point of contention is whether hominins accessed fleshy or largely defleshed carcasses, i.e., whether hominins were getting complete or nearly complete carcasses through hunting or aggressive scavenging (which are essentially indistinguishable archaeologically), processing the fauna at archaeological sites followed by carnivore (e.g., hyena) consumption of the residues (a hominin to carnivore two-stage model), or whether a three-stage model of felid consumption of flesh off a carcass, hominin passive scavenging and processing of bones for within-bone nutrients, followed by hyena scavenging of residues including long bone epiphyses, most accurately reflects the predominant mode of faunal usage at FLK Zinj. This distinction is significant, because it provides a measure of whether hominins were handling faunal packages able to feed multiple individuals or marrow-processing bones likely to satiate a single individual (Blumenschine, 1991; Isaac, 1978; Rose and Marshall, 1996). Blumenschine and colleagues clearly favor the three-stage model, while other authors generally favor the two-stage model. Several lines of evidence provide tentative support for the two-stage model, at least for FLK Zinj.

The first line of evidence is that bones with high economic value *when fleshed* (vertebrae, ribs, innominates, and scapulae) are well-represented in the FLK Zinj assemblage (38% MNE from Bunn and Kroll, 1986; see also Capaldo, 1997; Domínguez-Rodrigo, 2002; Lupo and O'Connell, 2002; Potts, 1988). This probably underestimates the number of axial and girdle parts transported to the site because their fragile nature (low structural density) makes them susceptible to compaction (Lyman, 1994), and they are often consumed by scavenging carnivores (Capaldo, 1997, 1998; Marean et al., 1992). The reasonably high frequency of axial and girdle parts likely signals the acquisition of fleshy carcasses by hominins (without a cooking/grease-rendering technology, they are of low economic utility defleshed; Lyman, 1994; O'Connell et al., 2002). The recovery of bones from every region of the ungulate skeleton in reasonably high proportions at FLK Zinj and other Oldowan sites supports the view that meaty carcass packages were transported to these sites (Bunn and Kroll, 1986; Oliver, 1994; Plummer et al., 1999; Potts, 1988).

Complete long bones occur in many of the Bed I archaeological assemblages (Potts, 1988), and may be another indirect indication of hominin access to fleshed carcasses. Carnivores abandon complete bones when satiated from flesh, particularly if group size is small and the prey is not fat-depleted (Bunn and Ezzo, 1993; Domínguez-Rodrigo, 2002; Potts, 1988). The high frequency of complete bones, particularly metapodials (which contain the least marrow of the limb bones), may reflect hominin neglect of some within-bone nutrients due to satiation from flesh (Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003).

As seen above, actualistic experimentation over the last 15 years has become one of the primary methods for addressing issues of hominin carcass acquisition, both in the Oldowan and later in time. The experimental modeling done up to this point has often been meticulous, but frequently the scope of these experiments has been too limited to produce the far-reaching conclusions about hominin behavior that are claimed. A relevant example is the use of midshaft tooth-mark frequency to infer the timing of carnivore access to a carcass, one of the pillars of the felid-hominin-hyena model of prey utilization that was argued to characterize the FLK Zinj assemblage (Blumenschine, 1991, 1995; Capaldo, 1997; Selvaggio, 1998; Domínguez-Rodrigo, 2002; Lupo and O'Connell, 2002). Given the wide array of actors that could have tooth-marked the Oldowan faunal assemblages, including felids, hyenids, canids, and the hominins themselves, the confident application of models predominantly using hyenas as the sole tooth-marking agent seems premature. Experiments have not frequently been conducted using the appropriate actors in the appropriate order of felid-hominin-hyenid. This is particularly troubling, given that recent work suggests that hyenas and large felids damage bones in different ways and possibly with very different tooth-mark frequencies, and it is the frequency of midshaft marks that was used to diagnose early carnivore access to carcasses (Domínguez-Rodrigo et al., in press; Pobiner and Blumenschine, 2003). Intraspecific variation has not been adequately assessed: for example, how do gross bone damage and tooth-mark frequency vary in lions, leopards, spotted hyenas, wild dogs, and jackals with changes in group size, predator to prey ratio, habitat, season, and ecosystem? How broadly applicable are damage data (particularly frequency data) collected from living, predominantly generalist taxa under a very limited set of experimental conditions going to be in application to fossil predator guilds with many extinct, specialist taxa (Table 4) whose behavior is incompletely known?

How certain can we be that high midshaft tooth-mark frequencies invariably reflect primary defleshing of bones by a large carnivore, rather than tooth marking by (potentially smaller) carnivores scavenging hammer stone-processed bones? The quantification of isolated "inconspicuous" tooth marks is an essential element of their methodology (Blumenschine and Marean, 1993; Capaldo, 1997), yet these marks can be produced by an extremely broad array of taxa (Domínguez-Rodrigo and Piqueras, 2003). There are no criteria for attributing most tooth marks to taxon, but it might be possible to attribute tooth pits to carnivore size class (Domínguez-Rodrigo and Piqueras, 2003; Monahan, 1999; Selvaggio, 1994; Selvaggio and Wilder, 2001). Analysis of tooth pits might provide a sense of the size range of carnivores consuming tissue from an assemblage, but findings would probably be biased towards the larger carnivores more likely to bite forcefully enough to create pits on the size 3 and larger mammal bones that form the bulk of the Bed I Olduvai archaeological faunae. Tooth scores, on the other hand, can be created by a variety of taxa, and these might be harder to size-class (Monahan, 1999). Given that large carcasses draw a succession of carnivores in Africa today and that the potential for interspecific competition among African carnivores is generally high (Caro and Stoner, 2003; Creel and Creel, 2002; Kruuk, 1972; Schaller, 1972), it is reasonable to think that Oldowan occurrences also attracted a variety of carnivores (Potts, 1988). If hominins did not completely consume the carcasses they processed, either because of on-site competition with carnivores (Potts, 1988) or satiation (Domínguez-Rodrigo, 1999b, 2002), or if in the course of defleshing carcasses with stone tools they left scraps of flesh on bone midshafts (Domínguez-Rodrigo, 1997, 1999b), the possibility of midshaft tooth-marking occurring *after* hominin processing would exist. The possibility that the hominins themselves may have tooth-marked some bones is also generally not considered (Domínguez-Rodrigo, 1999b; Oliver, 1994). While it is often not possible to unambiguously determine the timing of carnivore tooth-marking vs. hominin butchery, it is clear tooth-marking following hominin processing did take place at FLK Zinj. Hammer stone damage *preceded* tooth-marking in 63 of 65 long bone (mostly midshaft) fragments where the order of damage agents could be determined (Oliver, 1994, personal communication).

Finally, while there is ambiguity with interpreting flesh yield from cut-mark frequencies (Lupo and O'Connell, 2002; Pobiner and Braun, 2004), the distribution and frequencies of cut marks documented by Bunn and Kroll (1986) and Oliver (1994) are more consistent with the defleshing of substantial amounts of muscle tissue (Bunn, 2001; Domínguez-Rodrigo, 1997, 2002; Lupo and O'Connell, 2002) than with removal of small tissue scraps from passively scavenged felid kills (Dominguez-Rodrigo, 1999a). The balance of available evidence (reasonably high frequencies of axial and girdle bones and complete long bones, cut-mark distribution, and evidence that at least some tooth-marking occurred on midshaft fragments *following* hominin processing) suggests that the hominins forming the FLK Zinj assemblage often had access to carcasses with substantial amounts of flesh. The argument by Bunn and Kroll (1986) that they acquired carcasses through small mammal hunting combined with active scavenging of larger prey is consistent with this conclusion.

However, with the exception of Potts (1988) and Bunn (1986), the above series of studies sought to explain the formation of an Oldowan assemblage from a single level of a single site at a single locality: FLK Zinj. Recent research suggests that by approximately 2 Ma, there was considerable variability in the environments used by Oldowan hominins (Plummer and Bishop, 1994; Plummer et al., 1999; Sikes, 1994). We should expect variation in the frequency and mode of hominin acquisition of prey, reflecting differences in habitat structure and resource distribution, predator feeding adaptation, and predator to prey ratio, among other things. The obvious implication is that many other assemblages in addition to FLK Zinj need to be carefully scrutinized in order to fully document the breadth and extent of Oldowan carnivory.

A ZOOARCHAEOLOGICAL VIEW FROM ANOTHER SITE: KANJERA SOUTH, KENYA

The in-progress zooarchaeological analysis of fauna from Kanjera South provides some interesting points of comparison with the Bed I Olduvai datasets. Artifacts and fauna have been recovered from the basal three beds in the stratigraphic sequence (from oldest to youngest, KS-1 to KS-3), with dense concentrations of both artifacts and fauna in KS-2 and KS-3. The 175 m^2 Excavation 1 is the largest excavation to date, and has yielded approximately 3000 fossils and 4500 artifacts with 3D coordinates from a one meter thick sequence. As noted in the preceding discussion of Oldowan hominin paleoecology, the ca. 2.0 Ma Kanjera archaeological sites were deposited in a relatively open context, in contrast to the grassy woodland inferred for FLK Zinj from isotopic data (Sikes, 1994). Aside from fossils and artifacts recovered from thin, patchy conglomerates, water flow does not appear to have been the primary agent of accumulation of the archaeological materials in KS-2 and KS-3 (Plummer et al., 1999). The artifacts must have been deposited by hominins, and butchery marks directly links some fossils to hominin activity. The spatial association of the artifacts and bones, some with hominin damage, in KS-2 and KS-3 strongly suggests that hominins were the primary agent collecting and processing the archaeological fauna. The presence of carnivore damage confirms that other creatures modified the fossil assemblage.

Mammals make up more than 99% of the assemblage lifted with 3D coordinates. Bovids make up the bulk (88%) of the taxonomically identifiable specimens analyzed thus far (n = 1343) from the excavated faunal sample, followed by equids (10%) and suids (1%). One striking aspect of the fauna from Excavation 1 is that, compared with Bed I Olduvai, a large proportion of the assemblage consists of small (<72 Kg) mammals. This is well demonstrated by our preliminary size classing of the Excavation 1 mammal samples (Table 6). Small mammals on average make up 20% of the Olduvai Bed I assemblages studied by Potts (1988), with 55% medium mammals and 25% large or very large mammals. In contrast, 39% of the Excavation 1 NISP is from small mammals and only 1% from large or very large mammals. The substantial percentage (16%) of the Excavation 1 assemblage that in our initial size classing fell at the boundary of Potts' small and medium size classes further exemplifies the difference in the size distribution of the Kanjera fauna versus those found in the Bed I Olduvai assemblages.

The proportion of juvenile individuals within the small size class is also high relative to the Olduvai samples (approximately 50% in our preliminary assessment, versus an average of 25% for five Bed I assemblages; Potts, 1988). The overall sense of the Excavation 1 zooarchaeological samples is that they contain a higher proportion of small and frequently immature mammals than do the Bed I Olduvai assemblages. One hypothesis currently being tested by J. Ferraro is that hominins were the primary behavioral agent accumulating the small mammal remains, and that they had early access to them. If detailed taphonomic analysis supports this hypothesis, there would be a strong possibility that the size class 1 and 2 mammals found at Kanjera were hunted by Oldowan hominins. Small mammals rarely survive primary consumption by large carnivores (Bunn and Ezzo, 1993; Blumenschine, 1987) and according to ethnoarchaeological studies are easier to obtain compared to larger taxa (Yellen, 1991). For the portions of the assemblages linked to hominin activity, age profiles, damage patterns and (if obtainable) season of death will be used to assess acquisition strategies and determine whether they differed by size class (e.g., early access (hunting?) of size 1 and 2 mammals and later access (scavenging) of size 3 and larger mammals) and season (e.g., size 1 and 2 mammal hunting year round versus size 3 mammal dry season scavenging).

How does our preliminary analysis of the Kanjera fauna compare with FLK Zinj? As was the case for the Zinj excavation, the bounds of the artifact and fossil distributions were not reached at Excavation 1, so the sample under analysis may be a small part of what is present in situ. The Zinj assemblage represents a relatively discrete event (ten years or less) while our initial analyses suggest that hominins were intermittently attracted to the Excavation 1 locale for a much longer period of time. Excavation 1 preserves bones and artifacts that accumulated at multiple time intervals during the deposition of approximately 1 meter of sediment, suggesting multiple, intermittent episodes of activity. On-site competition with carnivores may have been less intense at Kanjera than Zinj, given the high frequency of size 1 and 2 bones at the former locality. If small mammal hunting is suggested by the Kanjera zooarchaeological analysis, it may provide some clarity to the pattern of faunal acquisition at FLK Zinj and other Bed I levels. Even though size 3 mammals predominate, there are a substantial number (MNI = 12 according to Bunn and Kroll, 1986; 10 according to Potts, 1988) of size 1 and 2 mammals at FLK Zinj. Bunn and colleagues (Bunn, 1986; Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Bunn, 2001) have argued that the small mammal component at FLK Zinj was hunted; others (Blumenschine, 1995; Capaldo, 1997, 1998; Cavallo and Blumenschine, 1989) have argued that passive scavenging of leopard kills was more likely. Early access to size 1 and 2 mammals from an open context unlikely to provide cached carnivore kills would strengthen the likelihood of small mammal hunting in at least some populations of Oldowan hominins.

It is perhaps notable that one other late Pliocene Oldowan faunal sample, the 2.3 Ma Lokalalei 1 in West Turkana, Kenya, also has a high proportion of size 1 and 2 mammals, though a detailed taphonomic analysis has not been carried out (Kibunjia, 1994). Investigation of more zooarchaeological samples is needed to clarify the variation in frequency and mode of hominin access to carcasses through the entire timespan of the Oldowan.

THE OLDOWAN DIET

The salient, archaeologically observable food resource in the Oldowan diet is meat (here referring to all soft tissue within the body, e.g., muscle, viscera, brains, and marrow). Large mammal bones with stone tool-induced modification are coeval with the oldest archaeological traces at 2.6 Ma, indicating that butchery is a component of the Oldowan as soon as tools appear (de Heinzelin et al., 1999; Semaw et al., 2003). There is currently no way to directly address the plant food component of the Oldowan diet, and researchers investigating Plio-Pleistocene plant resource utilization rely heavily on observations of hunter-gatherer and nonhuman primate plant food choice (Lee, 1979; Peters and O'Brien, 1981; Peters, 1987; Rodman, 2002; Schoeninger et al., 2001a; Sept, 1986; Stahl, 1984; Vincent, 1985), coupled with information on tooth size and shape, mandibular biomechanics, enamel structure, and enamel microwear (Grine, 1981, 1986; Teaford et al., 2002; Ungar, 2004). Plant foods are of critical importance to African tropical foragers, and it is likely that Oldowan hominins predominantly relied on plant foods as well. That being said, animal tissue does make up a considerable proportion of the tropical hunter-gatherer diet (e.g., 50% of mean annual caloric intake in the Hadza, Tanzania, 33% from the !Kung San, Botswana) (Lee, 1968; O'Connell et al., 2002), a substantive shift from the 5% or less of the annual caloric intake meat contributes to the chimpanzee (*Pan troglodytes*) diet, the most proficient hunter within the extant nonhuman catarrhines (Plummer and Stanford, 2000; Stanford, 1996). In humans, animal tissue provides a high-value currency for sexual negotiation with females, for provisioning of offspring and kin, and for reciprocal exchanges (Blurton Jones, 1987; Hawkes, 1993; Hawkes et al., 1991; McGrew and Feistner, 1992; Hill and Kaplan, 1993).

It is often argued that during the course of human evolution, increased consumption of animal tissue was a component of dietary change that fueled body size increase and brain expansion in the genus *Homo*, and was intimately associated with the development of a sexual division of labor and paternal investment in mates and offspring (Isaac, 1978; Lovejoy, 1981; McGrew, 1992; Stanley, 1992; Oliver, 1994; Aiello and Wheeler, 1995; Milton, 1999). Thus, discussion of the Oldowan diet has historically focused on meat acquisition, as it was a shift toward increased meat consumption that is one of the defining characteristics of human dietary evolution. The implicit assumption seems to be that the contribution of meat was greater than that seen in chimpanzees, but potentially less than what has been documented in African hunter-gatherers. Also considered below is a recurrent minority theme in the paleoanthropological literature, that high-quality plant foods, such as USOs, and not vertebrate meat, were the keystone resource that fueled the evolutionary transformation to *H. erectus* (O'Connell et al., 1999; Wrangham et al., 1999).

Wild plant foods commonly eaten by baboons, chimpanzees, and humans in Africa can be classified into broad categories, including flower buds (carbohydrates, some protein), fleshy fruits (carbohydrates, some protein, lipids), nuts/nut-like oil-seeds (lipids, protein), seeds/pods (carbohydrates, protein, lipids), leaves (protein, some carbohydrates), stems/pith (some protein, lipids) and USOs (carbohydrates) (Gaulin, 1979; Hladik and Chivers, 1994; Peters and O'Brien, 1981, 1994). Typically, nonhuman primates use fruit as an energy source, supplemented by seeds, leaves, and/or invertebrate/vertebrate tissue for protein and lipids (Hladik and Chivers, 1994). Extant *Papio* sspp. provide useful analogs to examine the ecological determinants of foraging behavior and diets in a large savanna primate without any cooking technology (Altmann, 1998; Altmann and Altmann, 1970; Barton et al., 1996; Hill and Dunbar, 2003; Whiten et al., 1991). This is a relevant exercise, because fossil *Papio* and *Homo* frequently co-occur, suggesting habitat overlap in the past (Bobe and Behrensmeyer, 2004), and extant hunter-

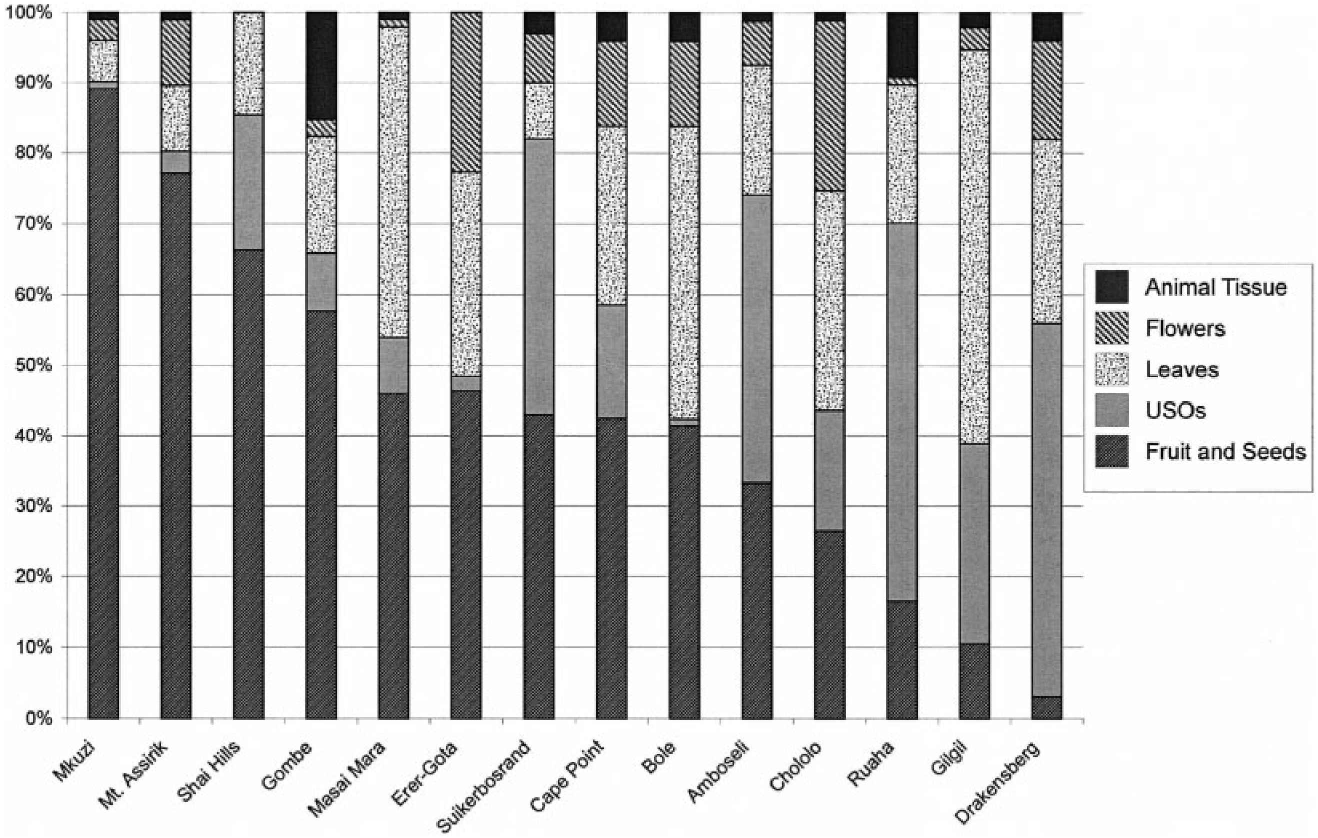

Fig. 3. Variation in modern *Papio* spp. diet. Data from Hill and Dunbar (2002).

gatherers and baboons eat a similar range of foods, from fruit to USOs (Peters and O'Brien, 1981). In 15 baboon populations across Africa, the proportion of feeding time devoted to fruits and seeds increases as mean annual temperature and plant productivity increase. Feeding time devoted to fruit and seeds is inversely related to that spent on USOs. The time spent feeding on USOs increases as temperature decreases and rainfall becomes more seasonal. These and other data compiled in Hill and Dunbar (2003) suggest that fruits and seeds are selected preferentially when available, and that USOs and leaves are important fallback foods when fruit and seed availability declines (e.g., during the dry season). Figure 3 shows the range of *Papio* dietary variation across Africa and demonstrates that there is not a single "*Papio*" diet: diets range from a predominant reliance on fruit (Mkuzi, South Africa) to diets emphasizing USOs and leaves (Ruaha, Tanzania), based on the local environment. Similarly, we ought to expect that there would not be a single "Oldowan" diet. The proportion of meat and various plant foods in the diet probably varied with local environmental conditions and possibly (at times when more than one stone tool using hominin was present) by taxon.

Nutritionally dense foods and hominin evolution

A high-quality diet is a characteristic of humans, and provides energetic support for our large brain. Human brain metabolism accounts for 20–25% of the resting energy demands of an adult, far more than what is seen in nonhuman primates (Leonard and Robertson, 1992, 1994). Human body composition appears to accommodate the metabolic costs of growing and maintaining a large brain: humans have a lower-than-expected muscle mass when compared to other primates, lowering the total metabolic costs of the body apart from the brain (Leonard et al., 2003). Metabolic costs might also have been offset through reduction of the gastrointestinal tract in humans (Aiello and Wheeler, 1995). The high metabolic cost of the human brain is an even greater issue in infants under 10 kg, where brain metabolism accounts for more than 60% of the resting metabolic rate (Leonard et al., 2003). Human infants have higher levels of body fat at birth than any other mammal, and gain fat at a high rate in the first year of life in order to provide energy stores for brain metabolism (Cunnane and Crawford, 2003; Leonard et al., 2003). Energy requirements stay elevated during infancy, necessitating breast milk and quality weaning foods for normal physical and cognitive growth.

There is a strong relationship between brain size and dietary quality in primates (Leonard and Robertson, 1994; Leonard et al., 2003). *Australopithecus* and *Paranthropus* had cranial capacities equivalent to or exceeding chimpanzees (*Pan troglodytes*), suggesting that these hominins had very good diets by nonhuman primate standards. The first major increase in absolute and relative hominin brain size occurs with *H. habilis* and *H. rudolfensis* (Table 2) (McHenry, 1994; McHenry and Coffing, 2000). *H. erectus* did not have a relatively larger brain than earlier forms of *Homo*, but did have a larger body and an absolutely larger brain size. This indicates that all forms of *Homo* had richer diets than any living nonhuman primate, and frames the discussion not in terms of whether high-quality foods were eaten, but what they were. Various authors (Aiello, 1996; Aiello and Key, 2002; Aiello and Wells, 2002; Aiello and Wheeler, 1995; Leonard and Robertson, 1992, 1994, 1997, 2000; Leonard et al., 2003; Milton, 1999) discussed the evidence for a higher-quality diet in *Homo* relative to the australopithecines, particularly with the emergence of *H. erectus*. This shift was probably accomplished by increasingly focusing on foods with high nutrient density, meaning foods that provided high nutrient and/or energy per unit volume. Indeed, the consumption of hard-to-acquire, nutrient-rich foods across several trophic levels is seen by some to be the key component of the modern human dietary adaptation (Kaplan et al., 2000; Leonard et al., 2003; Schoeninger et al., 2001a).

In addition to the carbohydrate-rich fruits that are a core component of the primate diet, three additional categories of nutritionally dense foods suggested by archaeological data, studies of nonhuman primates and hunter-gatherers, and nutritional analyses are nuts and seeds, USOs, and vertebrate meat. These are considered in turn below. However, it should be noted throughout this discussion that not nearly enough nutritional data have been collected on wild plant foods in Africa, or on returns from different tissues within African ungulates (by taxon and season). This dearth of information (and the frequent reliance on nutritional information from domesticates) hinders the evaluation of different dietary hypotheses within human evolution.

Nuts and seeds

The thick enamel, large molar area, and low relief of *Australopithecus* and *Paranthropus* molars suggest that they were at least occasionally cracking hard, brittle objects such as seeds and nuts in their jaws (Teaford et al., 2002; Ungar, 2004). The microscopic pitting of *P. robustus* teeth is also consistent with at least occasional bouts of hard-object feeding (Grine, 1986). Nut and nut-like oil seed-producing trees are broadly distributed across sub-Saharan Africa, and produce fruit frequently consisting of both an edible mesocarp as well as protein- and fat-rich seeds (Peters and O'Brien, 1981; Peters et al., 1984; Peters, 1987). Nuts and seeds are often available during the dry season, when fleshy fruits and other plant foods other than USOs are declining in abundance (Peters et al., 1984). For example, the fruit and seeds from the baobab tree (*Adansonia digitata*) are important dry-season food for the Hadza (Schoeninger et al., 2001a). The fruit, also eaten by baboons, provides energy as well as calcium and vitamin C. Seeds from the fruit are pounded into flour and when eaten provide a rich source of fat and protein (5 of 8 essential amino acids) (Schoeninger et al., 2001a). Mongongo trees (*Ricinodendron rautanenii*) provide both fruit and nuts (which humans roast), are high in protein and lipids, and were a staple food of the !Kung San (Lee, 1979). It is unlikely that hominins would have specialized in nuts and seeds, due to the seasonality in their distribution, probable competition with other large primates and a diverse group of suids (Peters, 1987), the lack of microwear evidence for a strong hard-object preference (particularly in *A. africanus*) (Grine, 1986), and isotopic evidence for a broad-spectrum diet in *A. africanus* and *P. robustus* (Sponheimer and Lee-Thorp, 2003) and presumably other hominins as well (Wood and Strait, 2004). However, nuts and seeds could have provided an important supplement to the diverse array of foods *Australopithecus*, *Paranthropus*, and *Homo* were eating (Goren-Inbar et al., 2002; Murray et al., 2001; Peters, 1987; Schoeninger et al., 2001a, 2003; Sponheimer and Lee-Thorp, 2003). They also hypothetically provide a dietary bridge to increased meat-eating. Schoeninger et al. (2001a) suggested that hominins with large hindguts and sizable cecal bacterial colonies (as inferred for *Australopithecus*; Aiello and Wheeler, 1995) would not have tolerated a rapid shift to high meat diets (though for a discussion of meat feeding experiments with chimpanzees, see Milton, 1999). Schoeninger et al. (2001a) proposed that nut and seed consumption in the lineage leading to *Homo* would have reduced the amount of dietary fiber and increased lipid dependence to the extent that the small intestine would have enlarged over time while the cecum reduced. This reconfiguration of the gastrointestinal tract would have preadapted the lineage for a diet with increased animal fat and protein.

Underground storage organs

Plants producing USOs such as tubers, rhizomes, and corms are abundant in savanna settings, can be found in large patches, are a good source of carbohydrates and moisture (though with more inedible fiber than domesticated tubers), are unaffected by grazing and fire, can be collected by hand or with the aid of a digging stick, and are available year-round, including the dry season (Hatley and Kappelman, 1980; O'Connell et al., 1999; Peters and O'Brien, 1981; Vincent, 1985; Wrangham et al., 1999). USOs are potentially the most abundant plant food resource available through the dry season (Foley, 1987). Hunter-gatherer groups worldwide in tropical and temperate latitudes utilized cooked USOs as a key carbohydrate source. Two recent models emphasizing USOs as a food staple challenged the view that increased meat-eating was the key dietary shift in the transition from *Australopithecus* to *H. erectus* (O'Connell et al., 1999; Wrangham et al., 1999). Both of these evolutionary scenarios assume that *H. erectus* could control fire, and that it was used to roast USOs to denature toxins and increase their digestibility (Stahl, 1984; Wandsnider, 1997). This newly acquired food (cooked USOs) provided a reliable, calorically dense resource that helped fuel body size increase and brain expansion and provided the day-to-day subsistence base to support the much riskier activities of hunting and scavenging. Other primates, particularly baboons, utilize USOs, often as a dry-season fallback food (Altmann, 1998; Hill and Dunbar, 2003; see above), and some USO consumption seems possible for fossil hominins.

Vertebrate tissue

Because meat is important in the diets of many human groups, and the processing of faunal materials is the single demonstrable function of Oldowan tools from their first appearance in the archaeological record (e.g., Blumenschine, 1995; Bunn and Kroll, 1986; de Heinzelin et al., 1999; Oliver, 1994; Potts, 1988; Semaw et al., 2003), and because stone tool-assisted butchery is seen as an important element in the transformation from *Australopithecus* to *H. erectus* (Aiello and Wheeler, 1995; Anton et al., 2002; Shipman and Walker, 1989), vertebrate meat has been viewed as an evolutionarily important resource for some time (Blumenschine, 1987; Bunn and Kroll, 1986; Foley, 1987; Isaac, 1978; Leakey, 1971; Lee and DeVore, 1976; Milton, 1999). Milton (1999) provided a useful review of the nutritional importance of meat from an evolutionary perspective. Meat is a high-quality food, whether consumed raw or cooked. Animal tissues provide an easily digestible (more easily digestible than plant protein) source of all amino acids, fatty acids, and many essential vitamins and minerals, including iron, calcium, iodine, sodium, zinc, vitamin A, many B vitamins, and vitamin C (Milton, 1999). Cyanogenesis is a common plant defense mechanism, and many staple human domesticates contain cyanogenic parts (Jones, 1998). Cyanide poisoning can often be averted through cooking, but intake of animal protein may have been critical for the consumption of cyanogenic but energy-rich wild plant foods prior to the controlled use of fire, as the amino acids methionine and cysteine assist in detoxifying cyanide (Jones, 1998; Milton, 1999). Human children require foods of high nutritional value, due to their large brains and high nutrient and energetic demands during growth, and this was probably also true of the development of weaned *H. habilis*, *H. rudolfensis*, and *H. erectus* children (Aiello and Key, 2002; Leonard et al., 2003). The relatively large increase in brain size for all species of early *Homo* suggests that meat would have been an important constituent in the diet of their weaned children.

Several researchers (e.g., Blumenschine, 1987; Foley, 1987) argued that Oldowan meat consumption was concentrated during the late dry season, when the most abundant woodland and shrubland plant food resources were depleted and large herds of ungulates would have congregated around permanent water sources. Poor forage quality and overgrazing around waterholes would have left ungulates weakened and relatively easy to kill by carnivores, and the remnants of these kills could then have been scavenged by stone tool-wielding hominins.

Perspectives on the Oldowan diet

Debate on the Oldowan diet typically does not revolve around the types of food eaten (it is generally assumed that fruits, seeds, nuts, USOs, and meat would have been consumed), but tends to center on the evolutionary significance of meat vs. a nutritionally dense plant food, especially USOs. Those favoring USOs argue that abundance and predictability in the landscape as well as high caloric value (especially when cooked) make them a more likely fuel for the evolutionary transition to *H. erectus* (O'Connell et al., 1999, 2002; Wrangham et al., 1999) than meat. Some favoring USOs have also called for a revised view of the economics of hunter-gatherer subsistence practices. Pair-bonding and food-sharing within the context of a sexual division of labor was one of the key components of the vision by Isaac (1978, 1984) of the activities being carried out at Oldowan sites or "central places," as they came to be called.

Within the last decade, human behavioral ecologists have had a spirited debate over male foraging practices in tropical hunter-gatherer groups, with two camps being formed (Panter-Brick, 2002). The first camp argues that the model of male big game hunting as paternal provisioning of meat to dependent female(s) and offspring that was so influential in the thinking of Isaac (1978, 1984) needs to be revised (Bird, 1999; Hawkes, 1991, 1993, 1996; Hawkes et al., 2001; Hawkes and Bleige Bird, 2002). Meat from large game is typically widely shared and so does not preferentially benefit the family of the hunter who made the kill. Moreover, big game hunting is a risky strategy in hunter-gatherers (due to unpredictability of acquisition and variability in return rate), and if males were truly trying to maximize caloric returns for provisioning purposes, they should be carrying out a mixed strategy of plant food foraging and small game hunting (Hawkes et al., 1991). Rather than being paternal investment, large mammal hunting is a form of competitive display that males carry out as mating effort that just so happens to provide benefits to the group.

The alternate view holds that the hunter-gatherer adaptation is based on the exploitation of large, nutrient-dense, difficult-to-acquire food packages, including large mammals. These are high-quality resources (protein and fat) that would be difficult for women and children to acquire on their own and that require skills taking years to master. It sees flexibility in the contributions of different ages and sexes, but the bottom line is that male provisioning yields the greatest energy component and most of the protein in the diets of most tropical foraging societies (Kaplan et al., 2000), that even in societies used to exemplify the competitive display strategy, male provisioning provides crucial resources during the reproductive history of a woman (Marlowe, 2003), and in many mid- to high-latitude societies, males were the main or sole food providers (Kaplan et al., 2000; Marlowe, 1999, 2001).

What is important here is not the resolution of this debate, but to note that in every hunter-gatherer society, meat provides nutrients that are important for female reproductive success, no matter how the socioeconomics of meat distribution are modeled. That being said, neither meat nor USOs are likely to have formed the preponderance of Oldowan hominin diet(s). Modern humans can only meet a maximum of 50% of their energy needs through metabolizing animal protein, and that is only with prey that also provide substantial quantities of fat (Aiello and Wells, 2002; Speth, 1989; Speth and Spielmann, 1983). Such a heavy reliance on animal tissue is unlikely in hot, dry climates, where prey tend to be more fat-depleted than in temperate climes, where the elevation in resting metabolic rate and increased water demand from a high meat diet would have deleterious effects on thermoregulation and water budgeting, and where plant foods are frequently available year-round. USOs are valuable carbohydrate sources, but would not alone provide a full complement of amino acids or micronutrients necessary for adults, or the even richer supply of protein, lipids, and micronutrients necessary for child development once encephelization increased. Moreover, arguments for the importance of tuber utilization developed from studies of modern hunter-gatherers in marginal, semiarid (annual rainfall approximately 500 cc, but with significant variation in rainfall amount) environments where USOs provide one of the few reliable resources during long dry seasons and where the low frequency of large mammal acquisition is partially a result of low large mammal biomass (Hawkes et al., 1997, 2001; Lee, 1979; O'Connell et al., 1999). In modeling hominin food choices, habitat usage, and population densities, semiarid environments similar to where the Hadza and San live today were considered "demographic sinks," occupied by hominins but not reproductively self-sustaining (O'Brien and Peters, 1999; Peters and O'Brien, 1994). Savannas with higher rainfall would have provided more opportunities for high-quality plant foods in addition to tubers (e.g. fruits, seeds, and nuts; see also the *Papio* data above) (Hill and Dunbar, 2003; Peters and O'Brien, 1994) and a much higher large mammal biomass providing more frequent live animal or carcass encounters (Coe, 1980; Owen-Smith, 1999). While there is environmental variation during the span of the Oldowan in East Africa, well-studied localities such as Bed I Olduvai and the Turkana basin generally appear to have been wetter, higher biomass settings during the Plio-Pleistocene than the areas inhabited by most African hunter-gatherers today (Blumenschine, 1987; Bobe and Behrensmeyer, 2004; Cerling and Hay, 1986; Cerling et al., 1988; Fernandez-Jalvo et al., 1998; Plummer and Bishop, 1994; O'Connell et al., 2002).

A further complication with the argument that USOs were a prime mover in hominin evolution is that it requires hominin control of fire for cooking at or just before the first appearance of *H. erectus*. While several claims for hominin control of fire were made for Africa between 1–1.5 Ma (e.g., Bellomo, 1994; Clark and Harris, 1985; Brain and Sillen, 1988; Gowlett et al., 1981), they were met with some skepticism (e.g., Bunn, 1999), with the oldest secure hearths from an archaeological context dating from 0.2–0.4 Ma in Europe (James, 1989). Recent argument for the controlled use of fire at 0.79 Ma in Israel is provocative, and may push hominin control of fire back to the beginning of the middle Pleistocene (Goren-Inbar et al., 2004). That would still leave at least a 1-Ma interval in Africa during which time hundreds of thousands of fires would have been lit to roast tubers, leaving no definitive evidence in Pleistocene sediments that do seem to record naturally occurring fires (Clark and Harris, 1985). Finally, even if USO roasting was occurring in the deep past, the nutritive value of wild tubers consumed by the Hadza appear to be significantly lower than was originally reported (Schoeninger et al., 2001b), undercutting the claim that USOs were the dietary keystone they were claimed to be.

In summary, what seems to best fit with human nutritional studies, the anatomical evidence for early *Homo* (particularly *H. erectus*), the archaeological evidence for acquisition of meat and marrow-yielding carcasses at what appear to be fairly high frequencies, and the variable but uniformly high quality of living hunter-gatherer diets all incorporating meat is that there was an increased meat intake with *H. habilis sensu stricto* and probably even more so with *H. erectus*, and that meat *in combination with a variety of high-quality plant foods* was probably the hallmark of the *H. erectus* diet. It is certainly likely that by 1.6–2.0 Ma, when sites were distributed from northern to southern Africa and from East Africa possibly west to the Democratic Republic of the Congo, Oldowan diets varied in their food constituency, depending on the range and relative availability of plant foods in the environment (e.g., the density and seasonal availability of fleshy fruits, nuts, and USOs), and on features of the local mammalian community that would have influenced hunting (e.g., encounter rates reflecting large mammal biomass) and scavenging (the number of carnivore taxa, their specific prey preferences and feeding adaptations, and the predator to prey ratio) opportunities. The strong possibility that there were at least two hominin taxa forming Oldowan sites (*H. habilis sensu stricto* and *H. erectus*) from ca. 1.6–ca. 2.0 Ma suggests that different dietary signals could be preserved archaeologically, based on subtle differences in foraging strategy.

BRIDGING SUBSISTENCE AND SOCIALITY

I believe the following conclusions can reasonably (but not incontrovertibly) be made about Oldowan hominin site formation and socioecology. Artifact and bone distributions indicate that hominins were repeatedly drawn to specific points on the landscape that possessed attractive resources (e.g., trees for shade, shelter, and food, and lithic raw material). The zooarchaeology of sites from Bed I Olduvai suggest that for this locality at least, carcass access may have been reasonably frequent. The MNI of about 50 prey individuals from FLK Zinj (a true minimum, because the assemblage was not excavated to completion) may have been accumulated over 5–10 years, suggesting that minimally 5–10 carcasses were processed per annum at this spot alone. Given that more than one “favored place” was likely used in a year, Bed I Olduvai hominins appear to have had regular access to carcasses. Meaty carcasses were acquired through confrontational scavenging or hunting, and on-site competition with carnivores appears to have been low. Size class 3 mammal carcasses (115–340 kg) or carcass parts were most commonly acquired, providing far more tissue than a single individual could consume, particularly if *H. habilis* (35 kg) was the hominin forming the assemblage. The predatory guild in the late Pliocene/earliest Pleistocene was about twice the size of the modern African carnivore guild, and predator density was likely higher than today. Competition with large carnivores may have favored group cohesion and coordinated movement, goal-directed transport of carcass parts to specific points on the landscape beyond the closest refuge, cooperative behavior including group defense, active, diurnal foraging with both hunting and scavenging, and the ability (using stone tools) to rapidly dismember large carcasses so as to minimize time spent at death sites (Foley, 1987; Lewis, 1997; Oliver, 1994; Rose and Marshall, 1996; Van Valkenburgh, 2001). Encephelization in earliest *Homo* beyond that seen in *Australopithecus* represents the first major increase in hominin cranial capacity, possibly related to increased incorporation of animal tissue into the diet. Increased ranging in warm, dry habitats in *H. habilis* sensu stricto is suggested by the nasal morphology of KNM-ER 1813 (Franciscus and Trinkaus, 1988) and the possibility of femoral elongation in OH 62 (Haeusler and McHenry, 2004).

Isaac (1978) emphasized the importance of food-sharing in Oldowan hominin socioeconomics. While there is no compelling evidence for a sexual division of labor in *H. habilis*, and plant foods may have been eaten as encountered, the acquisition, processing, and transport of carcass parts as envisioned here is likely to have been a group endeavor resulting in the sharing of meat (Rose, 2001). Morphological and life-history changes associated with the development of *H. erectus* provide additional theoretical evidence for the importance of a nutritionally dense diet including meat. It is likely that the increased size of *H. erectus* mothers (and consequently offspring) would have significantly impacted the reproductive strategy, social organization, and foraging strategy of these hominins. The increase in *H. erectus* body size itself could reflect selection pressures on both sexes related to the increased use of open environments that would have had a disproportionate effect on the smaller (female) sex (Aiello, 1996). The large body size of *H. erectus* combined with its longer, more linear form would have benefited thermoregulation and water balance under hot, dry conditions and decreased predation risk (Isbell, 1994; Ruff, 1991; Wheeler, 1991, 1992, 1993). Aiello and Key (2002) suggested that, relative to australopithecines, *H. erectus* females could have reduced the costs of reproduction by shortening interbirth intervals, shortening the period of lactation, and developing a support system whereby helpers assisted in weanling provisioning and feeding older dependent juveniles, thereby reducing the energetic burden on the reproducing female. Who these “helpers” were has been the subject of some speculation, with suggestions including the traditional view of male provisioning of pair-bonded female(s) and offspring, postreproductive grandmothers provisioning their daughters and grandchildren, older siblings provisioning younger ones, and male provisioning of females to reduce interbirth intervals and enhance mating opportunities (Aiello and Key, 2002; Hawkes et al., 1997, 1998; Isaac, 1978; Kaplan et al., 2000; O’Connell et al., 1999; Panter-Brick, 2002; Peccei, 2001). The important point here is simply to note that successful reproduction probably required a broader support network, including males. The evidence of high activity levels and inferential support for the human capacity for sweating and endurance running. Suggest that *H. erectus* was foraging in the heat of the day, including hunting and scavenging when other carnivores were resting. Whether fauna was acquired for male display, as paternal investment, or through the joint efforts of males and females, the carcasses processed by Oldowan tools were likely to have been incorporated into this support network. Possibly with *H. habilis*, but even more likely with *H. erectus*, meat-sharing was more extensive than the food-sharing seen in nonhuman primates (Feistner and McGrew, 1989) and a step toward the widespread sharing of food seen in modern humans.

ONSET OF THE OLDOWAN: BIG BANG OR GRADUAL DEVELOPMENT?

Did hominins flake stone or use unmodified stones prior to the onset of the Oldowan? For the last several decades, the oldest artifacts have been pinned to an age of about 2.5 Ma, and surveys of sediments older than this have not yet yielded artifacts (Panger et al., 2002; Semaw et al., 2003). Is the seemingly abrupt appearance of the Oldowan a sampling error, or was the initiation of flake production part of a behavioral complex involving lithic and food transport and the formation of debris concentrations that arose in toto? At this point it is impossible to tell, but ultimately this issue will help address the adaptive significance of the Oldowan technology at its inception. Isaac (1984) speculated that simple toolmaking and the use of nonfractured rocks could have long preceded the onset of the Oldowan. Others concur, and see the use of unmodified stones for nut-cracking in West African chimpanzees as indirect evidence that the last common ancestor between *Pan* and *Homo* used stones as tools (Mercader et al., 2002; Panger et al., 2002). Use of stone hammers and anvils for pounding (e.g., nut-cracking) inadvertently produces stone flakes (Mercader et al., 2002), but stone fracture would probably not have been habitually carried out until there was a recurrent need for sharp-edged tools. A “resource breakthrough” is implied because the stones themselves have no caloric value, and their incorporation into the foraging practices of a hominin suggests they either allowed access to a new food resource or allowed for more efficient processing of an existing resource (Potts, 1991). At that point, the inception of toolmaking could have been a threshold phenomenon, and the discovery that stone fractures predictably when struck (perhaps through the accidental flaking of a stone used for pounding nuts or some other plant food) would have immediately led to the two basic technological forms in the Oldowan: cores and flakes (Isaac, 1984). The initial flaking and utilization of stone may have had low archaeological visibility if tool use was dispersed in space and time, i.e., the resources being processed were not clumped or available over a long period of time, and/or stone itself was not habitually transported and so was not always available for tool manufacture. Chimpanzee foraging is tool-assisted; their foraging (and hence survival) is not dependent on tool use; tools are not manufactured far in advance of use, and they are not transported far (McGrew, 1992). Chimpanzee nut-cracking produces an archaeological record only because the nut-bearing trees persist for years, and the hammers and anvils are left in the vicinity of the trees and reutilized over time (Mercader et al., 2002). Similarly, if hominin foraging at the inception of chipped stone manufacture was not dependent at least seasonally on stone tool use, and activities requiring flaked stone were not spatially focused, then a prolonged period of pre-Oldowan stone tool utilization could have existed with very low archaeological visibility.

As Isaac (1978), Potts (1991), Schick (1987), and others noted, a key aspect of the Oldowan was the seemingly habitual transport of both tool stone and food across the environment. This suggests that by 2.0 Ma at least, stone tool usage had become a critical component of the adaptation of Oldowan hominins, and hominin foraging was tool-dependent. Even at 2.6 Ma, there are hints that the transport dynamics clearly represented by ca. 2.0 Ma at Kanjera, Olduvai, and Turkana were occurring (de Heinzelin et al., 1999; Semaw et al., 2003). As both lithic transport and faunal processing occur at 2.6 Ma, the possibility exists that the use of flaked stone was adopted rapidly and that the transport dynamics characterizing the Oldowan came into being in a short period of time.

Chimpanzees exhibit many cultural variants in tool use and behavior and different communities vary in whole suites of these (Whiten et al., 1999, 2003). It seems likely that tool use was not a species-wide phenomenon in the taxon that first flaked stone, but was developed in a single population or perhaps independently in several populations that may have already been using unmodified stones as tools. A plausible (but speculative) scenario for the development of the Oldowan technology in a hominin population as a “big bang” event is: 1) The resource breakthrough was animal-processing with stone tools, and hominin foraging practices transformed to incorporate more meat, through hunting but also through the tool-dependent processing of scavenged large mammal carcasses. This shift in foraging practice may have been precipitated by changes in the plant food resource base in the late Pliocene (see above), greater environmental heterogeneity, and increased large mammal biomass that may have increased live prey and carcass encounter rates and situated them more predictably in the environment. Obviously, once a lithic technology was developed, artifacts could have been used to process a wide variety of materials in addition to carcasses. 2) Habitual transport of stone was initiated in order to ensure constant access to tools. 3) Transport of carcass parts away from death sites was initiated to decrease competitive interactions with carnivores, move food requiring processing to adequate stores of raw material, refuges, and/or to easily defensible locations, and perhaps facilitate sharing. The stone tool-using hominin population(s) within a species may have had a selective advantage over those lacking a flaked stone technology. If the fitness advantage was great enough, stone tool technology might have spread relatively rapidly through the horizontal transfer of information (e.g., mate dispersal from a tool-using group to a group lacking lithic technology). If, as in chimpanzees today, the transfer of cultural information between communities occurred at a low rate or was nonexistent, cultural group selection may have led to the replacement of populations without a flaked stone technology by those that practiced it (Boyd and Richerson, 1985; Danchin et al., 2004).

At this point, it is impossible to choose between a separate development for stone technology and the transport dynamics that characterized the Oldowan, and the development of the lithic technology being coincident with the establishment of lithic and faunal transport. What is essential to addressing this question is a much more intensive, systematic investigation of the oldest Oldowan occurrences.

SUGGESTIONS FOR FUTURE RESEARCH

While a great deal has been learned about the Oldowan, the paucity of large, well-studied site assemblages from the full temporal and geographic span of the industry limits our ability to interpret the fundamental adaptation of hominins using stone tools, as well as the variability in their technology and subsistence practices. The necessary next step is to locate and excavate large primary-context assemblages that provide enough data to study Oldowan hominin behavior in its local and regional environmental context. This is true not only for the oldest occurrences, where the basics of stone tool transport and usage are very poorly documented, but also for later time intervals, where varying interpretations of a single site assemblage can dominate the literature. A greater emphasis on sourcing lithic raw materials, using petrological or geochemical methods, is critical for technological analysis. Lithic analysis combining more traditional technological and typological approaches with appropriate quantitative methods (e.g., reduction sequence quantification, Braun et al., 2003; material sciences analyses of artifact raw materials, Noll, 2000; calculation of flake perimeter to mass, Braun and Harris, 2003) may provide insights into the interplay between raw material physical properties, transport distance, artifact form, and potentially economizing behavior.

Much more can be done to standardize zooarchaeological approaches, starting with the fundamentals of the identification and coding of different surface damages (Blumenschine et al., 1996), all the way up to the appropriate design and use of actualistic studies for modeling Oldowan site dynamics (Domínguez-Rodrigo and Pickering, 2003; Domínguez-Rodrigo et al., in press; Lupo and O'Connell, 2002; Pobiner and Blumenschine, 2003). More detailed nutritional information on wild plant foods and their availability in different environments, as well as the nutritive value of different tissues within African ungulates (by taxon and season), is needed to better model hominin diets (Peters and O'Brien, 1981; Peters et al., 1984; Peters, 1987). Models of the hominin entrance into the carnivore guild need to be informed through better documentation of extant carnivore ecology, feeding behavior, and taxon-specific damage to bones, as well as the context and intensity of interspecific competition (Domínguez-Rodrigo et al., in press; Pobiner and Blumenschine, 2003). Given that the extant African carnivore community is depauperate relative to those of the past, the work of functional anatomists reconstructing the behavior and ecology of extinct carnivores needs to be better integrated into paleoanthropological research (Lewis, 1997; Van Valkenburgh, 2001).

Determining the season of faunal accumulation through stable isotopic analysis of enamel from developing teeth (Balasse, 2002; Balasse and Ambrose, 2002; Bocherens et al., 1996) and/or cementum analysis (Lieberman, 1994) is necessary to refine models of faunal acquisition. It is generally thought that hominin acquisition of fauna was a year-round activity (Potts, 1988), but several researchers suggested that the utilization of medium and large mammal carcasses peaked during the dry season, when many plant resources would have been depleted and herbivores themselves are under a considerable amount of stress (Blumenschine, 1987; Foley, 1987). Determining seasonality of death would allow us to test this “dry season crunch” model of faunal utilization, as well as note whether season of acquisition was patterned differently for smaller vs. larger mammals.

CONCLUSIONS

Research over the last several decades has provided a great deal of data and often contradictory interpretations regarding Oldowan hominin behavior and the adaptive significance of the first stone tools. A technologically simple method to dispense flakes from cores, the Oldowan provided a powerful means to cut, scrape, or pound a wide array of materials in the environment. Technological studies suggest that tool transport was habitual, certainly by ca. 2.0 Ma but perhaps as far back as 2.6 Ma. Butchery and consumption of meat and marrow appear to be characteristic of even the oldest Oldowan occurrences (de Heinzelin et al., 1999; Semaw et al., 2003). The appearance of the Oldowan coincides with generally cooler, drier, and more variable climatic conditions across Africa that probably led to a net decrease in woodland foods (deMenocal, 2004). Relative to the early and middle Pliocene, environmental restructuring may have increased the rate at which hominins encountered hunting opportunities and scavengeable carcasses. The incorporation of scavenged carcasses into the diet most likely occurred in hominin communities that already hunted small mammals, valued vertebrate tissue, and expanded their faunal search image to include prey that they themselves had not killed.

Probably at its inception, but certainly by ca. 2.0 Ma, the repeated transport of artifacts for use at different points on the landscape may have reflected pressure to curate or economize based on a current or projected need for stone. Oldowan sites are distributed across much of Africa after 2.0 Ma and apparently into Georgia as well, presumably reflecting range expansion by *H. erectus* across and out of Africa.

The largest, most meaningful assemblages of Oldowan debris are still derived from Mary and Louis Leakey's pioneering work at Olduvai Gorge well over 30 years ago (Leakey, 1971), and much discussion has focused on the very large FLK Zinj assemblage. There is a critical need to expand the sample of Oldowan site assemblages, particularly those preserving archaeological fauna as well as artifacts (Table 1). Though a variety of models of site formation have been proposed, there is a growing consensus on a number of points. High discard rates may have been more likely in rich, frequently visited foraging areas where the pressure to transport stone was relaxed (Schick, 1987). Once established, stone assemblages served as secondary sources of lithic raw material (Potts, 1984, 1988; Schick, 1987). Transport distances for lithic raw materials were sometimes on the order of several kilometers and less frequently up to 10 km, but this may represent cumulative movement over several separate transport events. Fauna was probably obtained through a combination of hunting and scavenging, and hominins accessed both flesh and within-bone nutrients. Faunal transport distances certainly varied, but it seems likely that some transport events were greater than a few hundred meters and more goal-directed than simply seeking the nearest patch of shade.

Carnivore modification was extensive but not intensive at FLK Zinj perhaps reflecting a low degree of carnivore competition on-site. Hominins at FLK Zinj appear to have had time to extensively process carcasses (Oliver, 1994), and may have sometimes had food in excess of need (Domínguez-Rodrigo, 2002). While the frequency of Oldowan hominin carnivory is difficult to assess (O'Connell et al., 2002), Bed I assemblages formed in thin paleosols suggest that carcass acquisition was fairly frequent and provided packages of tissue substantial enough to feed multiple individuals (Bunn and Kroll, 1986).

It is likely that at least two hominin taxa (*H. habilis* sensu stricto and *H. erectus*) made Oldowan tools, and both taxa may have been forming sites in the same depositional settings 1.6–2.0 Ma. Models of hominin energetics and dietary quality suggest that early members of the genus *Homo* and particularly *H. erectus* consumed high-quality diets, presumably including meat (Aiello and Wheeler, 1995; Leonard et al., 2003). While the general body plan of *H. habilis* is poorly known, the emerging picture of *H. erectus* is of a creature that was large and wide-ranging, with a high total energy expenditure (Aiello and Wells, 2002; Leonard and Robertson, 1997). Reconstruction of *H. erectus* reproductive energetics and socioeconomic organization suggests that reproductively active females received assistance from other group members. This inference, combined with archaeological evidence for acquisition of meaty carcasses, suggests that meat would have been a shared food. This is indirectly confirmed by nutritional analyses suggesting that the combination of meat with nutritionally dense plant foods was the likely diet fueling body size increase and encephelization in *Homo* (Leonard et al., 2003; Milton, 1999).

Given the enormous geographic distribution of Oldowan sites (Fig. 1) and the likelihood that *H. habilis* sensu stricto as well as *H. erectus* produced stone tools, it is reasonable to expect that Oldowan hominin lithic transport, curation strategies, and foraging behaviors varied across time and space, influenced by local ecology and stone tool raw material distribution. The adaptive significance of the first lithic technology has been incompletely explored, particularly at sites older than 2 Ma. Further detailed research is necessary to more clearly document whether hominins were accessing meaty carcasses over the geographic extent and temporal span of the Oldowan. Such research should provide clues to the frequency of carcass access, the likelihood of substantial sharing of meat, and the evolutionary significance of Oldowan carnivory.

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