Male strategies and Plio-Pleistocene archaeology[1]

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Archaeological data are frequently cited in support of the idea that big game hunting drove the evolution of early *Homo*, mainly through its role in offspring provisioning. This argument has been disputed on two grounds: (1) ethnographic observations on modern foragers show that although hunting may contribute a large fraction of the overall diet, it is an unreliable day-to-day food source, pursued more for status than subsistence; (2) archaeological evidence from the Plio-Pleistocene, coincident with the emergence of *Homo* can be read to reflect low-yield scavenging, *not* hunting. Our review of the archaeology yields results consistent with these critiques: (1) early humans acquired large-bodied ungulates primarily by aggressive scavenging, not hunting; (2) meat was consumed at or near the point of acquisition, not at home bases, as the hunting hypothesis requires; (3) carcasses were taken at highly variable rates and in varying degrees of completeness, making meat from big game an even less reliable food source than it is among modern foragers. Collectively, Plio-Pleistocene site location and assemblage composition are consistent with the hypothesis that large carcasses were taken *not* for purposes of provisioning, but in the context of competitive male displays. Even if meat were acquired more reliably than the archaeology indicates, its consumption cannot account for the significant changes in life history now seen to distinguish early humans from ancestral australopiths. The coincidence between the earliest dates for *Homo ergaster* and an increase in the archaeological visibility of meat eating that many find so provocative instead reflects: (1) changes in the structure of the environment that concentrated scavenging opportunities in space, making evidence of their pursuit more obvious to archaeologists; (2) *H. ergaster*'s larger body size (itself a consequence of other factors), which improved its ability at interference competition.

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Introduction

Men's big game hunting has long been identified as the primary catalyst for the evolution of early humans (e.g., Washburn & DeVore, 1961; Lancaster & Lancaster, 1983; Kaplan *et al.*, 2000). Allegedly pursued for the purpose of family provisioning, it is said to have enhanced the overall quality of ancestral hominin diets, favored increased intelligence and the development of larger brains, and promoted the emergence of uniquely human patterns of life history and social organization.

Archaeological data are commonly cited in support of this argument (e.g., Isaac, 1978; Isaac & Crader, 1981; Kaplan *et al.*, 2000). The earliest well-known sites are roughly the same age as the oldest definitely human fossils; many contain the remains of large animals; cut marks and impact scars on the bones themselves indicate that humans ate at least some of the meat and marrow (e.g., Isaac, 1997; Potts, 1988; Blumenschine, 1995). Many observers see these sites as the functional equivalent of modern hunter-gatherer base camps—places to which a variety of foods, including meat from big game, were brought to share with others (e.g., Isaac, 1978; Rose & Marshall, 1996). On the basis of this analogy, other characteristics long taken to be typical of modern behavior, including nuclear families and a sexual division of labor in support of offspring, are inferred for early humans as well (e.g., Isaac, 1978; Clark, 1997).

There are several good reasons to be skeptical of this "hunting hypothesis". Here we are concerned with just two. One is based on the observation that for many modern foragers big game hunting is a risky proposition, and commonly an arena for status rivalry rather than paternal effort (Hawkes & Bliege Bird, 2002). Even where meat from large animal prey makes up a sizable fraction of the diet, it is often not acquired reliably enough to meet the *daily* subsistence needs of hunters, and is seldom shared in ways that favor their own families (e.g., Hawkes, 1993; Hawkes *et al.*, 2001*a*). Moreover, whatever return rates are enjoyed typically depend on the use of relatively sophisticated projectile weapons (e.g., bow and arrow). If, as the archaeological record suggests, early humans lacked access to similarly effective weaponry, then the overall returns and day-to-day reliability of big game hunting would have been lower, probably much lower, than they are among moderns. Assertions about the role of hunting as an agent of evolutionary change are undercut accordingly.

The second basis for skepticism is the complementary argument that faunal assemblages at early sites are the product, not of big game hunting, but of relatively low-yield "passive" scavenging, defined as the culling of scraps from carcasses heavily ravaged and abandoned by their initial non-hominin predators (e.g., Binford, 1981; Shipman, 1986; Blumenschine, 1987). The same argument further holds that the early sites are not base camps, but simply convenient spots to which hominins sometimes carried bones from carnivore kills made in the immediate vicinity. If this argument is right, then inferences about nuclear families and paternal provisioning among early humans have no basis in the archaeology. More important, it means that meat from large animals probably cannot have been a key component in early human subsistence, let alone the main catalyst for the evolution of the genus: the quantities involved simply would have been too small.

Reactions to these challenges can be divided into two groups. Those in the first discount the ethnographic evidence against big game hunting as an effective provisioning strategy, reject the revisionist view of the archaeology, and reaffirm their faith in the original argument (e.g., Kaplan *et al.*, 2000). Big game hunting is identified as central to modern forager subsistence; the simplest reading of the archaeology indicates it was first pursued coincident with the origin of genus *Homo*; no other equally productive resources were exploited by humans at the same time; big game hunting is therefore the main force behind their initial evolution. Those in the second group dismiss the ethnography as irrelevant, flag the archaeology as the only reliable source of information on past human behavior, and pursue a more rigorous exploration of its character (e.g., Blumenschine, 1991*b*). Though they rarely appeal in detail to the hunting hypothesis, the fact that their analyses focus on the large animal remains suggests a continuing sense that meat eating was a primary factor in the evolution of early humans (e.g., Blumenschine *et al*., 1994; Capaldo, 1997).

Here we review key elements of this dispute, with special attention to the archaeological evidence so central to it. We begin with a brief outline of the problems posed by the emergence of genus *Homo*; then follow with a statement of the hunting hypothesis and a summary of the recent history of archaeological research related to its assessment. This leads us to consider the archaeology itself in greater detail, starting with a descriptive overview, then turning to a series of specific questions about early human procurement and handling of large animal prey. We are particularly concerned with inferences about how large carcasses were acquired, how often, and whether they were moved to sites that might be described as residential bases.

Our review leads us to conclude that neither hunting nor central place foraging is indicated archaeologically. Instead, we find the available data consistent with a pattern of opportunistic scavenging, probably of a more productive form than implied by the passive scavenging model. Though the oldest good evidence for this tactic, dated about 1·7–1·9 Ma, coincides with the appearance of *Homo ergaster*, its pursuit cannot account for distinctive features of the latter's anatomy, life history, and ecology. The indicated increase in scavenging ability is in our view more likely a *consequence* of early human evolution than its cause. It probably says more about male competition for status than it does about subsistence.

Throughout the paper, we make frequent reference to recent ethnographic and ethnoarchaeological observations among the Hadza, a modern East African foraging population (for background, see Blurton Jones *et al*., 1992, 1996, 2000 and sources cited therein). These observations challenge important elements of both the hunting hypothesis and the passive scavenging alternative. They also provide a basis for different behavioral interpretations of the archaeology. We rely on these observations, not because we imagine the modern Hadza to be "living fossils", but because knowledge of their behavior provides insight on the ecological opportunities and constraints that confronted early humans living in similar habitats. Potential reactions to those circumstances and their archaeological consequences can be anticipated accordingly.

Early *Homo*: questions raised

The ancestry of genus *Homo* can be traced to one of several Pliocene African taxa known collectively as australopithecines (sometimes "australopiths"). This category includes *Australopithecus*, *Ardipithecus*, *Paranthropus*, the newly reported taxon *Kenyanthropus* (Leakey *et al*., 2001), and the so-called "habilines", formerly assigned to *Homo*, now provisionally placed in *Australopithecus* (Collard & Wood, 1999, 2001; Wood & Collard, 1999). By modern human standards, most of these early hominins were small in stature, had long upper limbs, large molars and jaws, and, judging by the shape of their thoracic cavities, large digestive systems (e.g., Jungers, 1982; Stern & Susman, 1983; Johanson *et al*., 1987; McHenry, 1992; Aiello & Wheeler, 1995; Teaford *et al.*, 2002; see Klein, 1999; Wood & Collard, 1999; McHenry & Coffing, 2000; Wood & Richmond, 2000 for recent reviews). Though all were bipedal, overall body proportions suggest most had at least some arboreal capability (see McHenry & Berger, 1998 for recent review). Brain sizes were comparable to (in later forms, somewhat larger than) those of modern chimpanzees (McHenry, 1994). Analyses of dental micromorphology, eruption sequences, and skeletal development patterns indicate that they matured early relative to modern humans (e.g., Bromage & Dean, 1985; Smith, 1991; Dean *et al.*, 2001; Berge, 2002). Early maturation implies an overall life history pattern similar to that of chimpanzees, including late age at weaning and a maximum life span of 40–50 years (Smith & Tompkins, 1995; cf. Dean *et al.*, 2001). This in turn suggests little if any childhood provisioning and no extended post-menopausal longevity (Hawkes *et al.*, 1998).

The earliest clear-cut examples of *Homo*, called *H. ergaster* or "early African" *H. erectus*, probably appeared by about 1·7–1·9 Ma (Feibel *et al.*, 1989; Wood, 1991, 1992; White, 1995). Members of this taxon were taller and heavier than any of the australopiths, had smaller molars and mandibles, a smaller intestinal tract, and modern human limb proportions (e.g., Ruff & Walker, 1993; Ruff, 1994; Aiello & Wheeler, 1995; see also Klein, 1999; Wood & Collard, 1999; Wood & Richmond, 2000 for comparative review). Brain sizes were larger as well, but the increase in body size left the brain/body size relationship little different from the earlier hominin pattern (Collard & Wood, 1999; Wood & Collard, 1999). Collectively, these characteristics indicate reduced arboreal capability, more efficient terrestrial bipedality, broader foraging ranges, and a "higher-quality" diet. The dietary change may have involved greater reliance on foods that require less mastication and/or digestion, the adoption of more efficient pre-consumption processing technologies, or both (e.g., Aiello & Wheeler, 1995; Milton, 1999).

Life history characteristics also differed from those of the great apes and australopiths, and may have approximated those of modern humans (e.g., Smith, 1991, 1994*a*, *b*; Smith & Tompkins, 1995; Tardieu, 1998; Clegg & Aiello, 1999; Anton, 2002; cf. Dean *et al.*, 2001). Changes in dental eruption and epiphysial fusion sequences indicate relatively late age at maturity; life history models and patterns of correlated variation among living primates suggest significant post-menopausal longevity and relatively early age at weaning (Hawkes *et al.*, 1998; O'Connell *et al.*, 1999; Alvarez, 2000). Shorter birth intervals, relatively high fecundity, and sustained childhood provisioning are all implied (Hawkes *et al.*, 1998, 2002).

An important correlate of these changes was a huge increase in geographical range. By 1·5 Ma, *H. ergaster* had displaced australopiths over most, perhaps all, of their former territory, spread to areas previously unoccupied within Africa (e.g., Clark & Kurashina, 1979), and moved well beyond the continent, as far east as Indonesia and as far north as latitude 45–50° (Swisher *et al.*, 1994; Turner, 1999; Gabunia *et al.*, 2000; Larick *et al.*, 2001; Zhu *et al.*, 2001). Once achieved, the limits of this distribution remained relatively stable for more than a million years.

Most analysts agree that a shift in diet was crucial to the evolution of early *Homo*. The problem lies in identifying the resources involved and showing how their exploitation led to the indicated changes in morphology, life history, and ecology.

The hunting hypothesis

The idea that big game hunting drove the emergence of *Homo* has a long history

(Cartmill, 1994). Recent versions of the argument rely heavily on the work of Washburn and associates in the late 1950s and 1960s (e.g., Washburn & Avis, 1958; Washburn & DeVore, 1961; Washburn & Lancaster, 1968). Washburn's model was based on several apparent points of contrast between modern human foragers and terrestrial primates, mainly chimpanzees and savanna baboons. Highlighted were large brains, tool use, routine hunting of large-bodied prey by males, nuclear families with a sexual division of labor, and a pattern of extended juvenile provisioning, especially by fathers—all thought to be typical of hunter-gatherers, but unknown or poorly represented among other primates.

Washburn and colleagues attributed the appearance of this pattern to climate-driven changes in habitat. Cooler temperatures and increased aridity from the late Tertiary onward led to the expansion of open savanna at the expense of closed forest, reducing the availability of formerly important plant foods, but increasing the abundance and diversity of large-bodied herbivores. Ancestral hominin males purportedly responded by adding these animals to their prey lists, thereby producing a sharable resource, one that may have been especially important in dry seasons, when plant foods were limited. More hunting favored greater intelligence, larger brains, and increased reliance on technology. Larger brains posed an "obstetrical dilemma" for mothers, requiring that their babies be born earlier, in a more dependent state. The demands of childcare kept women from the chase, making them dependent on the hunting success of their mates. Nuclear families, a sexual division of labor, and paternal provisioning were all established as a result. Female fertility and offspring survivorship were enhanced; an extended period of juvenile dependence, increased learning ability, and greater behavioral flexibility all underwritten. (For recent restatements and elaborations, see Stanley, 1997; Clark, 1997; Lewin, 1998; Kaplan *et al.*, 2000; Stanford & Bunn, 2001).

Archaeological support

Archaeology played a key role in the development of this hypothesis. Excavations in East Africa during the 1960s and 1970s by Leakey (1971), Isaac (1997), and others revealed an archaeological record dating to about 2 Ma. In early reports, Isaac (1971, 1978; Isaac & Crader, 1981) drew special attention to sites marked by the presence of simple stone tools in association with the remains of many large animals, typically of several different species. Relying primarily on patterns in taxonomy and body part representation, Isaac identified these sites as "home bases", similar to those used by ethnographically known foragers. The large animal remains were read as clear evidence of repeated transport of meat to these sites to share with others. Additional elements of what was seen to be the modern human pattern, including nuclear families, a sexual division of labor, and paternal provisioning, were in Isaac's view strongly implied. The close coincidence between dates for these sites and those associated with fossils then identified as early examples of genus *Homo* provided what many regarded as strong support for the hunting hypothesis.

Some fundamental objections

As we said, this argument has been challenged in many ways, two of which are especially important. One is based on the observation that among modern meat foragers men's hunting and meat sharing practices are often inconsistent with the goal of family provisioning (e.g., Hawkes, 1991, 1993; Bird, 1999; Hawkes & Bliege Bird, 2002).

The Hadza provide a case in point. Hadza men are active, aggressive hunters, specializing in the pursuit of large animal prey (Bunn *et al.*, 1988; O'Connell *et al.*, 1988*a*,*b*). Operating in a game-rich, savanna woodland habitat, broadly similar to that of early Pleistocene East Africa, they encounter large animals, visually or by fresh tracks and other signs, nearly every day. Among those who are full-time foragers, meat provides an estimated 50% of mean annual caloric intake. Still, Hadza actually succeed in securing large animal carcasses by hunting or scavenging *only once every 30 hunter-days*, a *daily* failure rate of nearly 97% (Hawkes *et al.*, 1991). The fact that most camps include several hunters who routinely operate independently of one another reduces, but does not eliminate the risk of failure from a local group perspective. Records of over 250 camp-days of observation across all seasons over a period of five years show several stretches of a week or more with no meat from big game available (Hawkes *et al.* 1991, 1997, 2001*a*; see also Bunn *et al.*, 1988). Moreover, successful hunters do not control the distribution of meat from their own kills: most of it is claimed and consumed by individuals outside their own nuclear families (Hawkes *et al.*, 2001*b*). Neither the hunter's own effort nor his success rate affect the size or number of shares his household receives from others.

If Hadza men were primarily concerned with feeding their wives and children, they would do better by pursuing a broader range of resources, including small game and plant foods, both of which are much more reliably acquired and far more readily defended against the claims of others than are large animal carcasses (Hawkes *et al.*, 1991, 2001*b*). The fact that they rarely adopt this strategy indicates another goal for big game hunting, the most likely candidate being prestige, which affects their status relative to that of other men (Hawkes *et al.*, 2001*a*,*b*). Collectively, these observations, as well as similar ones made among other foraging groups (Dowling, 1968; Sackett, 1979; Hawkes, 1990, 1993; Wiessner, 1996; Bliege Bird *et al.*, 2001; Hawkes & Bliege Bird, 2002), undercut what has long been regarded as fundamental ethnographic support for the hunting hypothesis.

The second objection involves Isaac and others' reading of the early sites as evidence of hunting and central place foraging. As Isaac himself observed, the hunting component of the argument is open to question because of the absence of early evidence for projectile weapons. The bow and arrow, crucial to hunting success of many ethnographically known foragers, dates to the late Upper Pleistocene (<40 ka; Knecht, 1997); the earliest spears and projectile points to the late Middle Pleistocene (<500 ka; Kuhn & Stiner, 2001). Spears in particular might have been used much earlier, but if so it has not yet been demonstrated. Early humans or hominins might also have been able to take animals as large as mid-sized bovids by throwing stones (Isaac, 1987) or by running them to exhaustion (Carrier, 1984), but neither tactic is likely to have been productive enough to meet the demands of the hunting hypothesis.

Critics have pushed this objection further, arguing that the archaeology in fact provides *no* evidence of either hunting or home bases. In an influential review, Binford (1981) in particular suggested that some of the associations between stone tools and animal bones might be entirely fortuitous, perhaps largely the product of non human (mainly geomorphic) processes. Where hominin involvement with large animals was definitely indicated [specifically, by stone tool cut marks on animal bones (e.g., Bunn, 1981; Potts & Shipman, 1981)], Binford proposed that marginal scavenging, not big game hunting, was more likely implicated, the hominins involved having acquired only small quantities of meat and marrow from carcasses already heavily ravaged by their initial non-hominin predators. In Binford's view, there was no indication that meat or marrow were widely shared by hominins, that they were transported any great distance from the point of initial acquisition, or that they contributed significantly to hominin diets. From this perspective, not only big game hunting, but related inferences about nuclear families and paternal provisioning, are discounted completely.

The current state of play

The first objection, based on the modern hunter-gatherer research, has so far drawn little reaction, at least among archaeologists, mainly because of increasing skepticism about the relevance of ethnography to questions about early human evolution (e.g., Schrire, 1980; Wilmsen, 1989; Foley, 1996). Instead, attention and effort have focused on responses to Binford's critique, the goal being to develop better-warranted inferences about human behavior represented at the early sites. Much of this work has been "actualistic" in the sense that it has entailed the systematic investigation of processes responsible for the creation of sites and assemblages in the present, where their archaeological consequences can be observed directly. Inferences about the likely effects of these processes under different circumstances in the past are then drawn, and at least to some degree tested (e.g., Behrensmeyer & Hill, 1980; Binford, 1981; Brain, 1981; Gifford, 1981; Isaac, 1984, 1997; Lyman, 1984, 1994; Blumenschine, 1986, 1991*a*, 1995; Foley, 1987; O'Connell *et al.*, 1988*a*,*b*, 1990; Potts, 1988; Gifford-Gonzalez, 1991; Marean & Spencer, 1991; Marean *et al.*, 1992; Sept, 1992*a*; Bartram, 1993; Blumenschine & Marean, 1993; Lupo, 1994; Selvaggio, 1994; Stiner, 1994; Fisher, 1995; O'Connell, 1995; Tappen, 1995; Capaldo, 1997; Dominguez-Rodrigo, 1997, 1999*b*, 2001; Hawkes *et al.*, 1997; Blumenschine & Peters, 1998; Stanford & Bunn, 2001; Lupo & O'Connell, 2002).

As a result of this work, it is now agreed that most of the early sites reported by Leakey, Isaac and others are largely the products of hominin behavior: specifically, that hominins repeatedly acquired animal carcasses or parts thereof, moved them to these locations, and stripped them of edible tissue with simple stone tools. Beyond these points, opinions are strongly divided. Archaeologists most closely involved with the research generally continue to favor variants of the models articulated by Isaac and Binford. Sites originally identified as the equivalent of modern hunter-gatherer base camps are seen as either:

- *central places*, to which hominins carried substantial amounts of meat and bone from large animal carcasses acquired at appreciable distances, probably by means of hunting or "aggressive" scavenging (i.e., seizing a nearly intact carcass from one or more predators still engaged in eating it) (e.g., Bunn & Kroll, 1986; Plummer & Bishop, 1994; Rogers *et al.*, 1994; Rose & Marshall, 1996; Dominguez-Rodrigo, 1997; Bunn & Stanford, 2001); or
- *near-kill accumulations*, to which hominins brought varying but usually much smaller amounts of tissue, mainly long bone and cranial cavity contents "passively" scavenged from carcasses largely consumed and abandoned by predators quite close by (e.g., Blumenschine, 1991b; Marean *et al.*, 1992; Blumenschine & Marean, 1993; Selvaggio, 1994; Capaldo, 1997).

Those favoring the "central place" model usually take it that meat and marrow were widely shared with conspecifics. Most avoid further inferences about mating and reproduction, partly because of their skepticism about projecting models of recent hunter-gatherer behavior deep into the past, partly because of the absence of well-warranted, testable alternatives (but see Rose & Marshall, 1996). Those pushing the "near-kill accumulation" argument reckon that the amounts of edible tissue captured in any single scavenging incident were probably too small to be shared. Like their colleagues on the "central place" side, they too generally avoid inferences about other aspects of behavior, for essentially the same reasons.

Aside from the archaeologists, there is another party to this debate, important because their arguments are generally directed at a broader, but archaeologically less sophisticated audience (e.g., Tooby & DeVore, 1987; Barkow *et al.*, 1992; Leakey & Lewin, 1992; Stanley, 1996; Deacon, 1997; Kaplan *et al.*, 2000). Members of this group are either unaware of the controversy surrounding behavioral interpretations of the archaeology (e.g., Barkow *et al.*, 1992; Deacon, 1997), or frankly unimpressed with its potential implications (e.g., Kaplan *et al.*, 2000). In their view, the record can be read precisely as it was when first discovered: as clear evidence of big game hunting by human or hominin males and the transport of meat to residential bases to share with dependents, notably mates and offspring. Cautionary observations about the inconsistency of modern foraging and food sharing practices with assumptions about paternal provisioning, the inability of modern East African foragers to support themselves on a day-to-day basis by big game hunting, and the implications of the latter observation for the success of early humans pursuing similar strategies with less sophisticated technologies are either ignored or dismissed as irrelevant.

Questions emerging

Resolving these differences of opinion about the behavioral implications of the archaeology is crucial to any assessment of the hunting hypothesis. If Binford and others are right that it provides no evidence of access to large animal prey except by passive scavenging, then that hypothesis is refuted, at least with respect to early *Homo*. Unless large, heavily ravaged carcasses were acquired at very high rates, the flow of nutrients generated from this activity cannot have been sufficient to support the sharp changes in body size, life history, and ecology indicated for *H. ergaster*. If Binford is also right in thinking that the early sites represent near-kill accumulations rather than home bases, then archaeological support for related inferences about nuclear families and a sexual division of labor in foraging disappears as well. Other explanations for the origin of *Homo* and its distinctive life history and social organization must be given serious attention.

Even if Binford is wrong, and the initial reading of the archaeology as evidence of hunting and food sharing at central places is right, modern hunter-gatherer ethnography raises an important question: How often did the early humans responsible for these sites have access to large animal prey? Like all young primates, *H. ergaster* juveniles probably had to eat several times a day, *every* day. Like modern human children, they probably also relied on others to provide most of their food for years after weaning. The hunting hypothesis holds that early human males were the main source of this support, yet traditional East African hunters living in similar habitats today cannot meet this need, despite their use of sophisticated weapons. Though meat represents a sizable fraction of their families' *annual* caloric intake, it is not acquired reliably enough to satisfy the *daily* nutritional needs of their children. Unless *H. ergaster* was able to acquire the meat of large animals much more regularly than the modern Hadza, the sharp changes in diet, life history, and geography indicated by the fossil record must reflect increased access to some other food source.

This brings us to a detailed look at the archaeology. We begin with an overview of the material record, with special attention to the large animal bone assemblages; then consider the evidence for method and frequency of carcass access and the transport of parts to central places.

Archaeological evidence

Archaeological data on early hominin exploitation of large bodied prey are reported from 19 sites in the East African Rift (Table 1). Sixteen are in terminal Pliocene and early Pleistocene deposits—eight at Olduvai, seven at Koobi Fora, and one at Peninj. The remaining three (Kanjera South, Bouri, and Hadar/AL 666) are older.

The Olduvai, Peninj, and Koobi Fora sites have been reported in some detail (e.g., Leakey, 1971; Potts, 1988; Isaac, 1997; Dominguez-Rodrigo *et al.*, 2002). All contain the remains of many large animals, usually in association with simple stone tools of the Oldowan or Developed Oldowan Traditions. (Artifacts are absent at GaJi 5 and Bouri, but are indicated indirectly by the presence of distinctive cut marks on some of the bones.) At most sites, bones and stones are horizontally concentrated in one or more roughly circular patches ranging from 5–20 m in diameter. Vertical dispersal of material within such patches may be substantial, sometimes as great as a meter or more (Kroll, 1997). It is not clear whether this indicates long periods of accumulation, substantial amounts of post-depositional disturbance, or both (see below). It is also not clear whether the scatters exposed at each locality represent the absolute limits of small, well-defined sites; or, alternatively, whether they are parts of much larger entities (O'Connell *et al.*, 1992). [Data recently reported from Peninj suggest that the latter may be the more common pattern (Dominguez-Rodrigo *et al.*, 2002).] These uncertainties aside, it is generally agreed that many of these concentrations are high-density features, sometimes exceeding "background" counts of bone and stone by up to two orders of magnitude (Kroll & Isaac, 1984; Potts, 1988; cf. Blumenschine & Masao, 1991).

The animal bone assemblages themselves vary widely in size, from about 200 to >40,000 specimens. Numbers of at least minimally identifiable pieces (NISP) range from about 75 to 3500; minimum numbers of individual animals (MNI) from 5 to >50; minimum numbers of taxa (MNT) from 5 to >20. Taxa most commonly represented are mid-sized [so-called "class 3" (Brain, 1974; Bunn, 1997)] ungulates, mainly bovids, with adult body weights in the 100–300 kg range. Equids, suids, giraffids, hippopotamids and proboscideans are also frequently present. Most of these animals were prime-age adults at the time they died (Potts, 1988; Bunn, 1997).

Though not yet fully analyzed, one of the three older sites (Kanjera South) appears to be similar to those at Olduvai and Koobi Fora. The other two (Bouri and Hadar/AL 666) are smaller, and have so far yielded only limited evidence of hominin involvement with large animal prey.

Carcass acquisition

In principle, large animals or parts thereof can be acquired by hunting and/or one or both forms of scavenging, passive and aggressive. As indicated above, aggressive scavenging is defined as the seizure of prey from its original predator(s) before the latter would otherwise abandon it. Amounts of edible tissue gained by this tactic are highly variable, but can be substantial, sometimes amounting to complete or near-complete carcasses (e.g., O'Connell *et al.*, 1988*a*). Passive scavenging involves the acquisition

Table 1 Archaeological sites providing evidence of Plio-Pleistocene hominid carnivory

Site name	Locality	Stratigraphic unit	Age (Ma)	Context	Area exposed	Depth	Industry	No. of artefacts	No. of bones	Large mammal		
										NISP	MNI	MNT
Early Pleistocene												
BK	Olduvai	Upper Bed II	1·2	SC	114	1·5 m	DO	7220	2515	1444†	53†	12
MNK Main	Olduvai	Middle Bed II	1·4	LM/FP	92	1·4 m	DO	5315	1427	842†	10†	7
ST	Peninj	USC	1·5	SC	3500	<30 cm	DO	354	1563	1166	53	18
FxJj 20E	Koobi Fora	Lower Okote	1·6	FP	140	<1 m	O	1774	3123	417	21	14
FxJj 20M	Koobi Fora	Lower Okote	1·6	FP	135	<1 m	O	4391	4574	420	20	14
FxJj 50	Koobi Fora	Lower Okote	1·6	SC	193	<1 m	O	1438	2120	762	21	13
FxJj 64	Koobi Fora	Lower Okote	1·6	FP	40	<30 cm	O	45	578	111	5	5
GaJi 5	Koobi Fora	Upper KBS	>1·6	DL	50	<30 cm	O?	None	>200	76	10	9
Plio-Pleistocene transition												
FLKN 1/2	Olduvai	Upper Bed I	1·75	LM/FP	100	<60 cm	O	1205	>1700	2274	45	16
FLKN 6	Olduvai	Upper Bed I	1·75	LM/FP	37	50 cm	O	130	2258	614–740	22–35	13–14
FLK Zinj	Olduvai	Middle Bed I	1·76	LM/FP	290	<10 cm	O	<2647	>40,000	~3500	36–48	16–22
FLKNN 3	Olduvai	Middle Bed I	1·76	LM/FP	209	<10 cm	O	72	2261	390	34	14
DK 2	Olduvai	Lower Bed I	1·86	LM/FP	345	<70 cm	O	1163*	5422	832	41	22
DK 3	Olduvai	Lower Bed I	1·86		345	<10 cm	O		2433	518	36	22
FxJj 1	Koobi Fora	KBS	1·9	FP/DL	65	<50 cm	O	138	689	228	16	14
Fxjj 3	Koobi Fora	KBS	1·9	FP/DL	35	<50 cm	O	120	237	75	10	8
Late Pliocene												
Kanjera South	Kanjera	KS 1&2	>2·15	FP/SC	96	nr	O	>1642	>2320	nr	*nr*	*nr*
AL 666	Hadar	Kada Hadar	2·3	FP	2	10 cm	O	34	*nr*	nr	nr	*nr*
Bouri	Middle Awash	Hata	2·5–2·6	FP/LM	nr	nr	O?	None	>400	nr	nr	nr

Data on Koobi Fora sites from Feibel *et al.* (1989), Bunn (1994), Isaac (1997); on Olduvai from Leakey (1971), Gentry & Gentry (1978), Kroll & Isaac (1984), Bunn (1986), Bunn & Kroll (1986), Potts (1988), Walter *et al.* (1991), Tamrat *et al.* (1995), Monahan (1996*a*,*b*); on Kanjera from Ditchfield *et al.* (1999), Plummer *et al.* (1999); on Hadar from Kimbel *et al.* (1996); on Middle Awash from Asfaw *et al.* (1999), Heinzelin *et al.* (1999); on Peninj from Dominguez-Rodrigo *et al.* (2002).

Depositional context: DL, delta; FP, flood plain; LM, lake margin; SC, stream channel. Area exposed refers to the lateral extent of archaeological excavations, measured in square meters; depth to the vertical distance over which artifacts and associated fauna were encountered.

All stone artifacts are assigned to the Oldowan (O) or Developed Oldowan (DO) Industries, as defined by Leakey (1971) and modified by Toth (1985; see also Isaac, 1997). All counts of artifacts and animal bones refer to items recovered within the limits of archaeological exposures, except at GaJi 5, Peninj, and the Pliocene sites, where associated surface remains are also included.

Large mammal NISP refers to the number of (at least minimally) identifiable specimens present; MNI to the minimum number of individual large animals; MNT to the minimum number of large animal taxa.

*Artifact counts from levels 1 and 2 combined.

†NISP and MNI from BK and MNK do not include equids (see Gentry & Gentry, 1978; Monahan, 1996*a* for additional detail).

of carcasses already heavily ravaged and abandoned by other predators. Quantities of tissue acquired by secondary consumers are usually small, often amounting to little more than long bone marrow and brain cavity contents (Blumenschine, 1987).

In recent years, aggressive scavenging has come to be a commonly nominated tactic, especially among archaeologists who favor some version of the hunting hypothesis (e.g., Bunn & Ezzo, 1993; Bunn, 2001). It requires the ability to displace other predators, not necessarily to kill them. Simple harassment, say by stone throwing, might often have been sufficient. Some have objected to this suggestion, noting that since effectiveness at aggressive scavenging usually correlates with hunting ability among carnivores, including modern humans, early humans or hominins good at one should also have been good at the other. This might be partly right: a shower of rocks annoying enough to force a lion off a kill might also have brought down an antelope, at least on occasion. On the other hand, the ability to run an antelope to ground seems unlikely to translate quite as effectively in contests with large predators.

Given *any* evidence of the consumption of large animals by hominins, passive scavenging seems almost certain to have been among the tactics practiced. The direct costs of exploiting abandoned kills are low, and the post-encounter returns are better than those available from many other resources (Blurton Jones *et al.*, 1989; Blumenschine & Madrigal, 1993; Blurton Jones, 1993; Hawkes *et al.*, 1995, 1997; Lupo, 1998). The key question is whether carcasses were ever acquired in more complete condition, either by hunting or aggressive scavenging. This issue has generally been addressed by reference to two sorts of evidence: the *relative frequency of various prey body parts* found in archaeological sites, and *patterns in carnivore- and hominin-produced damage* across those parts.

Body part representation. Table 2 shows the distribution of body parts at the 12 sites for which pertinent data are available. Most assemblages (those in Groups 1 and 2, Table 2) are made up mainly of head and limb parts. With some exceptions, scapulae, pelves, vertebrae, and ribs are less well represented.

Some analysts see these data as evidence of hominin hunting (e.g., Isaac, 1978; Bunn & Kroll, 1986; Rose & Marshall, 1996). This inference is based on the belief that modern foragers routinely transport fully-fleshed limbs to base camps, but strip and discard axial parts other than heads at the kill, primarily as a means of reducing transport costs and maximizing load utility. The head-and limb dominated pattern allegedly produced as a result is sometimes referred to as the "schlepp effect" (Perkins & Daly, 1968). The implicit assumption is that if hominins responsible for these assemblages commonly acquired prey in less complete condition, they would have moved a different set back to base.

Critics have rightly observed that no ethnographically known foraging group actually moves prey body parts from kill sites to base camps as the "schlepp" model suggests (for descriptions and analyses of modern hunter-gatherer transport practices see Yellen, 1977; Lee, 1979; Binford, 1978; Bunn *et al.*, 1988; O'Connell *et al.*, 1988*b*, 1990; Bartram, 1993; Marshall, 1994; Monahan, 1998). Among the Hadza, for example, the pattern for mid-sized bovids like those that dominate most Plio-Pleistocene assemblages is just the reverse. Limbs are the elements most often stripped and discarded at or near kills; axial parts are frequently carried back to residential sites for further processing (O'Connell *et al.*, 1988*b*, 1990; Monahan, 1998; cf. Bunn *et al.* 1988). Early Pleistocene hominins may

Table 2 Body part composition (NISP) of Plio-Pleistocene and Early Pleistocene faunal assemblages (after Monahan, 1996*a*: Table 4.1; Bunn, 1997: Tables 8.16, 8.19)

	n	Skull	Vertebra	Rib	Scapula/ pelvis	Complete limb	Limb epiphysis	Limb shaft	Limb total	Manus/ pes
Group 1										
FxJj 1	235	68	2	8	2	0	1	18	19	2
Fxjj 3	75	64	0	3	0	0	0	29	29	4
FxJj 20E	381	50	1	3	1	0	3	28	31	14
FxJj 20M	391	62	5	5	1	0	3	19	22	6
Group 2										
BK	1444	33	5	11	3	nr	nr	nr	40	8
FxJj 50	739	13	7	38	1	0	3	36	39	3
FxJj 64	107	14	0	73	0	0	1	10	11	3
FLK Zinj	3513	28	5	18	2	0	4	38	42	5
MNK	842	34	7	7	5	nr	nr	nr	36	12
ST	1166	(see footnote)								
FLKN 6	402	38	14	4	4	3	12	2	17	22
GaJi 5	76	20	9	13	22	0	7	25	32	4

(*n*) is the number of identified specimens (NISP); all other columns are approximate percentages of (*n*). Discrete limb segment tallies are not available for BK and MNK; segment percentages from other sites are totaled for comparison. Sites are grouped by broad similarities in body part representation. Assemblages in Group 1 are similar to those in Group 2, except that they have been subjected to greater degrees of density-dependent attrition. Relatively high proportions of ribs and vertebrae at FxJj 50 and 64 reflect the presence of very large animals (size class 5 or 6; with adult body weights >900 kg). Rib fragments at FxJj 64 may represent a single highly fragmented element (Bunn, 1997:427). Though pertinent data from ST/Peninj have not yet been fully published, %NISP tallies for major element categories (skull=8%, axial=39%, appendicular=53%) are most similar to those in Group 2 (Dominguez-Rodrigo *et al.*, 2002).

not have done the same, but as yet there is no good reason to think they did the opposite.[2] Eliminating the "schlepp" model as a basis for interpretation leaves the standard argument about big game hunting based on body part representation groundless.

A counter argument, that early hominins most often acquired large carcasses in a heavily-ravaged state, is better warranted. Blumenschine (1987), a major proponent, observes that carnivores commonly attack large carcasses in a predictable manner, first consuming the internal organs, then stripping the meat from the upper hind limbs and pelvis, then working their way forward across the vertebrae, ribs, and upper front limbs. He further observes that lions feeding on mid-sized ungulates, like those most commonly represented at Olduvai and Koobi Fora, often abandon the remains with little or no flesh left, but with the brain and marrow cavity contents intact. If Plio-Pleistocene felids did the same, and no other consumers intervened, then hominins might have collected these items, moved them to convenient spots nearby (e.g., shaded areas), cracked the bones, consumed the contents, and moved on. If scavenging opportunities were common at certain points on the landscape, and hominins routinely exploited them, then over time large assemblages similar to most of those in Table 2 could well result (see also Binford, 1981:249–288; Blumenschine & Marean, 1993).

The problem with this argument is that it does not fully control for the effect of secondary consumers on assemblage composition. Hyenas are especially effective at stripping carcasses of "within-bone" nutrients, including grease-rich items (Binford *et al.*, 1988; Blumenschine, 1988; Marean *et al.*, 1992). Most analysts, including Blumenschine, see the high ratios of grease-poor limb shafts to grease-rich epiphyses at most of the early sites as clear evidence of hyena activity (Table 2). The argument is that, however the carcasses were acquired, hominins processed heads and long bones for their contents and discarded the resulting bone fragments, which were then culled—mainly for long bone epiphyses—by hyenas. But the same process should also have reduced the abundance of any other grease-rich elements (i.e., vertebrae, ribs, scapulae, and pelves) once present as well (Lyman, 1984). The fact that these parts are still represented in every assemblage (23% of NISP across all sites in Table 2), *despite* secondary consumption by hyenas, strongly suggests that they were more common in the bone sets initially deposited by hominins.

We can generate rough estimates of their original representation by reference to the minimum number of skeletal elements (MNE) recovered archaeologically, which can then be corrected for the impact of postdepositional attrition. Large, comprehensive MNE data sets, are available for just two sites, FLK Zinj and FLKN 1/2 (Bunn, 1986). Table 3 shows the counts for scapulae, vertebrae, ribs and pelves at both, along with an estimate of the minimum number of individual animals (MNI) represented by each element, and the relationship of that number to the highest MNI estimate for the site, based on parts that are more resistant to post-depositional attrition. Though MNE

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[2] Stiner (1991, 1994) summarizes a large body of evidence indicating that non human predators that transport meat and bones from large animal kills routinely favor limbs for removal whenever possible. Modern human foragers do the same where the transport distances are short; i.e., measured in tens of meters (e.g., O'Connell *et al.*, 1992). The question is whether humans would also do so where: (1) transport distances were much greater, (2) stone tools gave them opportunity to strip and discard relatively heavy bones or bone fragments in ways that improved transport efficiency, and (3) boiling technology, which allows the leisurely extraction of grease from axial parts at base camps and so encourages the differential transport of those parts (e.g., Binford, 1981; O'Connell *et al.*, 1990), was unavailable. It should be possible to answer this question through formal modeling (e.g., Metcalfe & Barlow, 1992), but pertinent quantitative analyses have not yet been reported.

Table 3 Numbers of low density skeletal elements at FLK Zinjanthropus and FLKN 1/2: recovered archaeologically *vs.* deposited initially

	FLK Zinj				FLKN 1/2			
	MNE	MNI	% of highest MNI for site (48)	Est % pre-ravaging	MNE	MNI	% highest of MNI for site (45)	Est % pre-ravaging
Scapulae	14	7	15	nd	29	14	31	nd
Ribs	31	2	4	>40	46	2	4	>40
Vertebrae	35	2	4	>40	56	2	4	>40
Pelves	18	9	19	38	15	8	18	36

MNE=minimum number of elements of each type recovered archaeologically (data from Bunn, 1986: Table 2); MNI=minimum number of individual animals represented by each element (MNE/number of elements of that type in a living animal); percentage of that value relative to the highest MNI estimate for the assemblage as a whole (data from Table 1 above); estimated representation of elements as initially deposited, prior to carnivore ravaging, based on experimental results reported by Marean *et al.* (1992). (Experimental data for scapulae unavailable.)

counts for vertebrae and ribs are relatively high (n=31–56), adjusting for the number of elements in a living animal lowers the resulting MNI estimates substantially. Only two animals would be required to account for these parts at each site, less than 5% of the highest MNI estimates made on other parts. Scapulae and pelves are better represented, making up about 15–30% of the highest MNI estimated for each assemblage. Marean *et al.*'s (1992) experimental data suggest that while the highest MNI estimates for these sites are unlikely to have been much reduced by post-depositional attrition, those for vertebrae, ribs and pelves are: pelves by a factor of two, vertebrae and ribs by 1–2 orders of magnitude. Conservatively speaking, this implies that 30–60% of the total number of animals originally deposited at both sites were represented by (among other elements) a pelvis, 40% or more by vertebrae and ribs.

Either as originally calculated or as adjusted for post-depositional attrition, the substantial representation of pelves has an important implication for arguments about the timing of carcass access. Fully fleshed, these are very high utility items, consistently among the most meat-rich body parts on any ungulate (Blumenschine & Caro, 1986). This is why they are almost always among the first parts consumed by carnivores. Once stripped of meat, however, they have little value to meat eaters other than as a source of grease, which would have been expensive for hominins to extract in the absence of boiling technology. The fact that pelves were moved even short distances from kill sites strongly implies that they were acquired by hominins while still at least partly fleshed, meaning the latter enjoyed at least occasional early access to large-bodied prey.

This reading draws additional support from Brantingham (1998), who observes that in bone assemblages created by non-human carnivores the order in which the accumulator gained access to carcasses may be indicated by the ratio of minimum number of prey skeletal elements to minimum number of individual animals (MNE/MNI) represented (see also Stiner, 1994). Where the accumulator is adept at hunting and aggressive scavenging, the ratio is relatively high. Where it gains access to large prey parts mainly by passive scavenging, the ratio is low. MNE/MNI values calculated by Brantingham for FxJj 50 and five sites in Bed I Olduvai fall within the ranges typical of assemblages created by wolves and spotted hyenas, both of which often enjoy relatively early carcass access.[3]

Damage morphology. Humans and carnivores damage the bones of their prey in the course of removing edible tissue. Experimental work indicates that variation in the frequencies of different types of damage may reflect the order of consumer access (e.g., Binford, 1981; Binford *et al.*, 1988; Marean & Spencer, 1991; Marean *et al.*, 1992; Blumenschine & Marean, 1993; Lupo, 1994; Oliver, 1994; Selvaggio, 1994; Blumenschine, 1995; Capaldo, 1997; Dominguez-Rodrigo, 1997, 1999*b*, 2002*a*; Bunn, 2001; Lupo & O'Connell, 2002; O'Connell & Lupo, 2002). For methodological reasons, confidence in interpretive

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[3] Marean (personal communication, 2002) questions the relevance of Brantingham's analysis, arguing that the non human assemblages to which the Olduvai and Koobi Fora remains were compared were tallied in ways that did not control for the selective consumption of long bone epiphyses by the carnivores (see also Bartram & Marean, 1999 for discussion of the effect in another context). Correcting this problem might increase the number of limb elements identified in these assemblages, and so raise the resulting MNE/MNI ratios. Assuming that the human-produced samples have already been handled correctly in this regard (Bunn & Kroll, 1986; Potts, 1988; Bunn, 1997), their MNE/MNI ratios would then fall lower on the revised non human carnivore scale, implying somewhat later access to carcasses, on average, than Brantingham's analysis suggests. Unless the proposed adjustment were very great (Stiner, 2002*b* argues that this is generally unlikely to be the case), the results should still be consistent with at least occasional early access on the part of humans responsible for these assemblages.

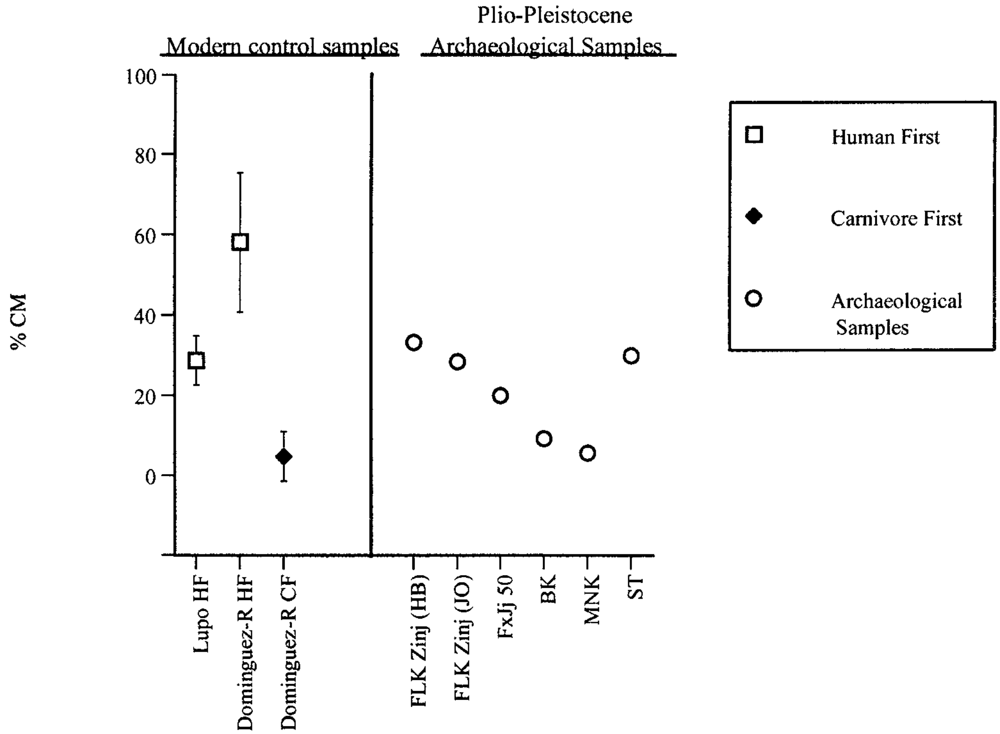

Figure 1. Percentages of upper limb midshafts cut marked (%CM): modern control vs. Plio-Pleistocene archaeological samples. Open squares indicate percentages of humerus and femur shaft fragments bearing one or more cut marks (means and standard deviations) in control assemblages handled first by humans (HF), then by carnivores; the solid diamond shows comparable data from control assemblages handled first by carnivores (CF), then by humans (Dominguez-Rodrigo, 1997: Table 2; Lupo & O'Connell, 2002: Table 8). Archaeological data from FLK Zinj (two estimates: HB=Bunn & Kroll, 1986: Table 4; JO=Oliver, 1994: Table 1); FxJj50 (Dominguez-Rodrigo, 2002*a*: Table 1), ST/Peninj (Dominguez-Rodrigo *et al.*, 2002: Table 14), BK and MNK (Monahan, 1996*b*). The value for BK was adjusted by Monahan (1996*b*: Table 6) to control for the effect of bone surface attrition. We made a similar adjustment to the raw data reported for MNK. See Lupo & O'Connell (2002) for additional detail and discussion.

utility of this finding must be limited, at least for the moment (see Lupo & O'Connell, 2002; Dominguez-Rodrigo, 2002*b* for discussion). Still, the following observations are important:

- In two sets of experiments, cut marks were found on about 30–60% of all upper limb (humerus and femur) shaft fragments handled initially by humans, then by carnivores (Figure 1; see also Dominguez-Rodrigo, 1997; Lupo & O'Connell, 2002). In a third set, where the order of access was reversed, cut mark counts were much lower: on average, less than 5% of all fragments marked (Dominguez-Rodrigo, 1997).
- In five sets of experiments, tooth marks were found on an average of 5–30% of all limb shaft fragments handled initially by humans, then by carnivores (Figure 2; see also Blumenschine, 1995; Capaldo, 1997; Dominguez-Rodrigo, 1999*b*; Marean *et al.*, 2000; Lupo & O'Connell, 2002). In four experiments where the order was reversed, tooth mark counts were much higher: on average, 45–80% marked (Selvaggio, 1994; Blumenschine, 1995; Capaldo, 1997; Marean *et al.*, 2000).

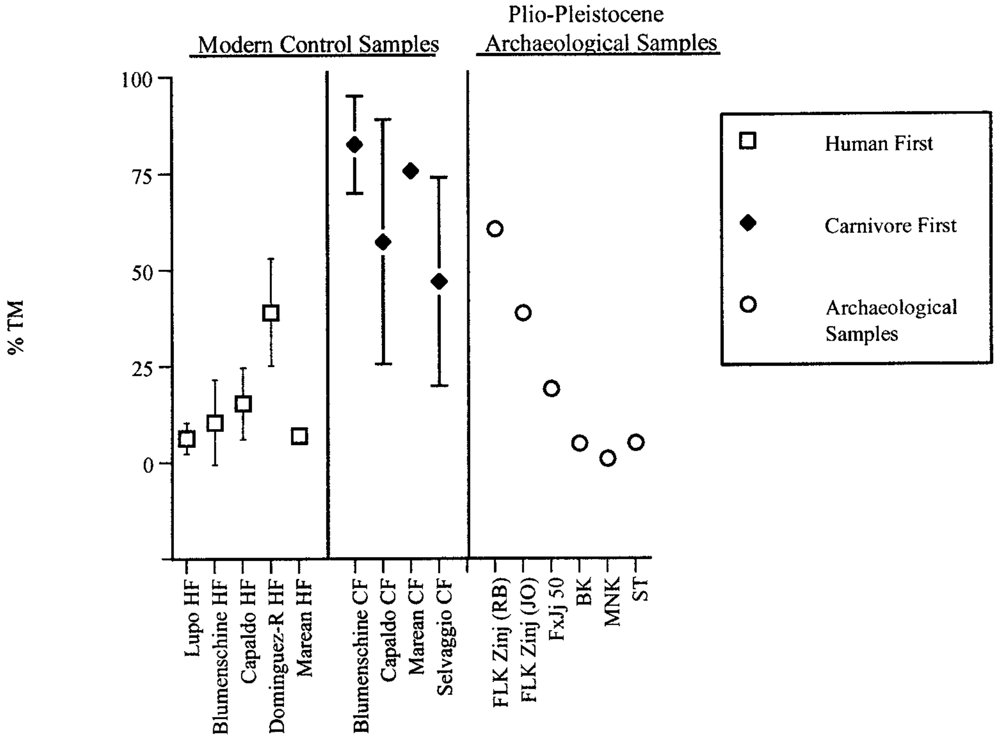

Figure 2. Percentages of all limb shaft fragments tooth marked (%TM): modern control vs. Plio-Pleistocene archaeological samples. Open squares indicate percentages of all limb shaft fragments bearing one or more cut marks (means and standard deviations) in control assemblages handled first by humans, then by carnivores; solid diamonds show comparable data from control assemblages handled first by carnivores, then by humans (Selvaggio, 1994: Table 2; Blumenschine, 1995: Table 3; Capaldo, 1997: Table 9; Dominguez-Rodrigo, 1999*b*: Tables 2–3; Marean *et al.*, 2000: Table 3; Lupo & O'Connell, 2002: Table 10). Archaeological data from FLK Zinj (two estimates: RB=Blumenschine, 1995: Table 3; JO=Oliver, 1994: Table 1); FxJj50 (Dominguez-Rodrigo, 2002*a*: Table 1), ST/Peninj (Dominguez-Rodrigo *et al.*, 2002: Table 13), BK and MNK (Monahan, 1996*b*: Table 7). Values reported for BK and MNK were increased by a factor of 50% to control for the effect of bone surface attrition (after Monahan, 1996*b*: 108). See Lupo & O'Connell (2002) for additional detail and discussion.

Archaeological assemblages dating as early as the Middle Paleolithic, and thought on other grounds to have been produced by human hunters, show patterns consistent with these experimental results: high cut mark counts on upper limb shaft fragments, low tooth mark counts on all limb shaft fragments combined (e.g., Marean & Kim, 1998).

Data from the early Pleistocene are less clear-cut. At FLK Zinj, the largest and by far the best preserved of the five assemblages for which relevant information is available, cut mark counts on upper limb shafts are pegged at about 30% (Bunn & Kroll, 1986; Oliver, 1994), essentially identical to the mean figure for sites produced by modern Hadza hunters (Figure 1; see also Lupo & O'Connell, 2002). Tooth mark counts on limb shafts overall are reported at about 40% or 60%, depending on the analyst (Oliver, 1994; Blumenschine, 1995). The 60% figure fits better with a carnivore-first model; the 40% value is ambiguous (Figure 2). At FxJj 50, tooth and cut mark values [19 and 20%, respectively (Dominguez-Rodrigo, 2002*a*)] are both consistent with a human-first model. At Peninj, 30% of the upper limbs shafts are cut-marked, 5% of all shafts tooth-marked (Dominguez-Rodrigo *et al.*, 2002), again consistent with a human-first model. Finally, at BK and MNK, both sets of counts are quite low (Monahan, 1996*b*). The 9% and 6% cut mark values are consistent with a carnivore-first model; the 5% and 1% tooth mark values with a human-first model.

Conflicting signals from these early sites almost certainly reflect problems with both the experimental controls and the damage pattern counts themselves (Lupo & O'Connell, 2002). That said, the match between experimentally-based expectations and archaeological data from much younger sites generates at least some confidence in the general approach. The best cases for early human access to carcasses in the Plio-Pleistocene are presented by FxJj 50 and Peninj. At FLK Zinj, high cut mark counts rule out passive scavenging as the primary mode of carcass access, but high tooth mark counts still indicate substantial carnivore involvement early in the consumption sequence. Hunting proficiency comparable to that seen among late Middle Pleistocene through modern humans is not indicated here. Though we lack a modern experimental referent, we suspect that aggressive scavenging by hominins on carcasses variably ravaged by carnivores might well generate the damage patterns reported for FLK Zinj, and perhaps for Peninj and FxJj 50 as well. The same explanation might also account for the data from BK and MNK, although the low absolute values for both tooth and cut marks undercut our confidence in this inference.

Home bases vs. near-kill accumulations

The assemblages themselves clearly signal at least minimal transport and accumulation by some agent. Fluvial processes are ruled out as the major contributor by patterns in body part representation and element orientation; non human carnivores are eliminated on both body part representation and damage morphology, specifically the absence of damage patterns typical of carnivore dens (Potts, 1988; Petraglia & Potts, 1994; Isaac, 1997). This leaves hominins as the only plausible option.

The notion that the early sites were hominin home bases is grounded on three aspects of the large animal bone assemblages: large numbers of individual animals, high taxonomic diversity, and high proportions of limb elements. High taxonomic diversity suggests to many that carcasses were acquired in a wide range of habitats, some at substantial distances from the sites at which their remains were ultimately deposited (Isaac, 1978; Plummer & Bishop, 1994). High percentages of limb elements are seen to be consistent with this inference, primarily by reference to the "schlepp model" (Isaac, 1978; Bunn & Kroll, 1986; Rose & Marshall, 1996). But since the "schlepp" model is itself unsupported, the home base inference fails on this count. As we will see shortly, the other two criteria—large numbers of individuals and high taxonomic diversity—are ambiguous.

The near-kill accumulation model takes two forms.[4] The first, proposed by Potts (1984, 1988), is based on the observation that in Africa today, large carcasses are often the setting for fierce, sometimes fatal competition among non human carnivores. The presence of a larger Plio-Pleistocene predator guild (Turner, 1990; van Valkenburgh, 2001) may have made for even more intense competition at the time the early archaeological sites were being created. Early humans successful at acquiring carcass parts, but wishing to escape the competitive atmosphere, may have moved their take to

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[4] Sept (1992*b*, 1998) suggests a third option; that the early sites were akin to the nesting areas used by modern chimpanzees (see also Fruth & McGrew, 1996). The behavioral correlates (especially with respect to meat eating and food sharing) and archaeological consequences of this interpretation are not yet fully developed.

safer spots nearby. The redundant use of many of these sites was allegedly determined by the presence of toolstone purposely cached there in anticipation of the need to process carcass parts.

Although elements of this argument are appealing (see below), the signature component, cached toolstone, is poorly warranted. Unless the quantities of meat and marrow acquired by early humans were very small (and so not worth moving at all), it should always have been cheaper to move stones to meat, rather than the reverse. In fact, detailed analyses of the early artefact assemblages indicate that hominins routinely carried toolstone with them as they moved about the landscape, often over distances of several kilometers, probably because of its utility in a wide range of tasks and settings, including (but not limited to) the dismemberment of large animals (Toth, 1985; Kimura, 1999). Assemblages at some sites lack stone tools of any kind (Table 1), even though the latter were clearly used there, as indicated by cut marks on bone surfaces (Bunn, 1994; Heinzelin *et al.*, 1999). If tool stone caching were a common practice, such sites should be rare. The fact that they have been recognized at all, despite the absence of eye catching artifacts, suggests that they may be fairly common (Bunn, 1994).

The second alternative is based in part on Binford's (1984:262–264) "routed foraging" model. According to this scenario, hominins routinely visited a range of locations in search of food, among them sites where predators frequently made kills, and where scavenging opportunities might often have been available. Recurrent visits over long periods of time, including the periodic transport of edible remains to the nearest shade, led to the creation of sometimes sizable accumulations of animal bones and the stone tools used in processing them.

Though some analysts claim that opportunities to hunt or scavenge large animals do not occur often enough at any given point on the landscape to allow assemblages like those listed in Table 1 to accumulate as Binford proposed, our experience with the Hadza shows otherwise (O'Connell *et al.*, 1988*a*,*b*, 1992; Lupo, 1993; O'Connell, 1997; Lupo & O'Connell, 2002).

Hadza process and discard large animal bones at three kinds of sites: residential base camps, and single and multiple carcass butchering stands. Sites in the third category are of special interest here. They are located on and around perennial water points, usually in stream channels. They are visited in all seasons, but are monitored most closely in the late dry, a 3–4 month period when surface water is otherwise scarce, and large ungulates and their various predators are drawn to the relatively few remaining sources. Hadza build hunting blinds on elevated ground immediately overlooking these waters and along trails leading to them, and shoot large prey as they move within range. They also monitor prey and predator traffic around these sites, and are especially attentive to evidence of predator kills and related scavenging opportunities, commonly signaled by circling vultures and distinctive predator calls. On evidence of such an opportunity, all Hadza who notice it move quickly to the site, sometimes from different directions, often over distances of several kilometers, and on arrival attempt to drive off any predators still present and secure the prey. Roughly 20% of all large carcasses acquired by the Hadza during our fieldwork were taken in this way, most in relatively complete condition, many at perennial water points.

However a carcass is taken at these locations, Hadza frequently move all or part of it to a shady spot close to the water for further processing, an exercise that typically involves the consumption of meat and marrow and the discard of stripped and marrow-cracked bones. The type and number of bones deposited at the butchering stand vary with the size of the animal, its

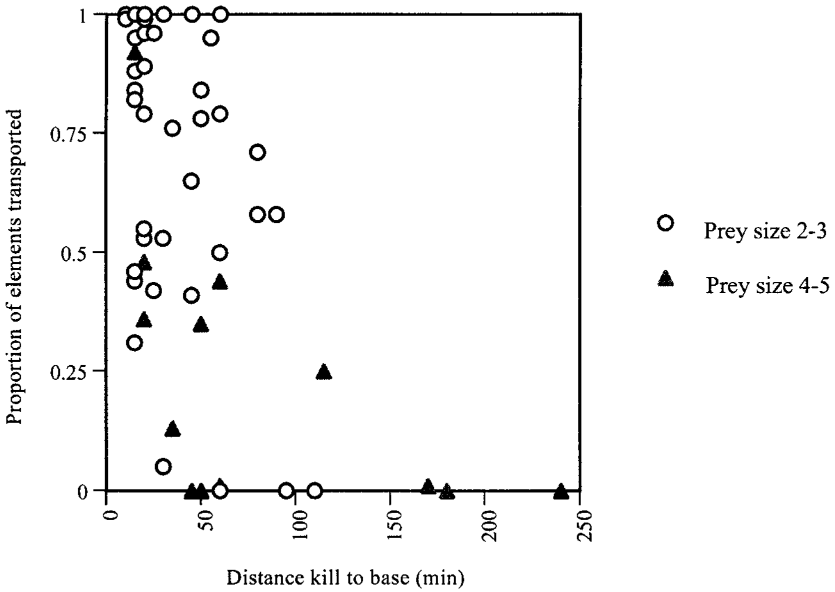

Figure 3. Relationship between distance (min) from kill site to base camp and proportion of skeletal elements transported. Sample includes 61 carcasses, each representing a single kill or scavenging event (Bunn *et al.*, 1988; O'Connell *et al.*, 1988*b*, 1990). Values on the horizontal scale indicate the distance from kill site to base; those on the vertical denote the proportion of skeletal elements moved from each carcass. (○) indicates prey with adult body weights 40–300 kg; (▲) those with weights >300 kg.

economic anatomy, the distance to the residential base, and the number of people available to assist in the butchery and help carry away parts (O'Connell *et al.*, 1988*b*, 1990). Broadly speaking, the larger the animal, the greater the distance to base and the fewer people available to help carry meat, the more likely bones are to be left either at the kill itself or at the nearby butchering stand (Figure 3).

Archaeological sites created as a result of these activities display several important characteristics:

- *They are found near perennial water points where Hadza never camp.* At the one best known to us, the site is defined as a 250 m long, 100 m wide section of perennially wet stream channel (Figure 4). Diffuse concentrations of bone debris up to 20 m in diameter, all produced by Hadza carcass processing activities, have been identified in several shaded areas along the channel margin.
- *They contain the remains of many individual prey.* Over 57 days of observation in the late dry seasons of 1984 and 1985, Hadza operating from base camps 1–2 km away killed at least six large animals at the site just described, and seized at least one, possibly two others nearly intact from lions. Bunn's group reports additional kills and aggressive scavenging incidents at the same site in late dry 1986 and again in 1988 (Bunn *et al.*, 1988; Bunn, personal communication, 1988). A surface collection from one frequently-used blind at this site yielded about 450 large animal bone fragments, representing a minimum of 300 separate skeletal elements and at least eleven individual animals, all from an area measuring about 10 m^2 (Lupo, 1993).
- *They contain taxa often identified as markers of diverse habitats.* Though this part of Hadza territory is covered by acacia woodland, prey identified as open country

Figure 4. Low oblique view of Hadza intercept hunting/multiple carcass butchering location (from O'Connell *et al.*, 1992). Principal feature is a perennial marsh, ca. 250 m long, formed in the channel of an intermittent stream which flows from lower right to upper left. Circles mark the locations of known hunting blinds; square indicates a spot where several carcasses were butchered. Other carcasses were butchered in shady locations elsewhere along the edges of the marsh. See Bunn *et al.* (1988), O'Connell *et al.* (1992), Lupo (1993), Lupo & O'Connell (2002) for additional details.

forms, notably plains zebra and alcelaphine antelope, are taken there often. In the surface collection just mentioned, impala, zebra, wildebeest, hartebeest, buffalo and warthog are all represented. All, including the alcelaphines and zebra, were acquired at this location, even though the nearest open grassland is 7–10 km away.

- *They are dominated by head and limb fragments*. Specimens in these categories represent more the 70% of all ungulate skeletal parts in the surface collection (Table 4).

Sites like these are not unique to the Hadza, but are also known from other parts of arid and semi-arid eastern and southern Africa (e.g., Crowell & Hitchcock, 1978; Brooks & Yellen, 1987; Dominguez-Rodrigo, 1999*b*). It is important to emphasize that they are not in any sense home bases. The common presence of large predators, especially in the late dry, makes them dangerous places, especially at night, even for hunters in thorn-walled blinds. Women and children rarely visit these locations after dark. Among the Hadza, base camps are almost always established in other settings, 10–20 minutes walk from permanent water, generally outside riparian habitats, especially in the dry season.

Consider the sites in Table 1 from this perspective:

- Many occur in floodplain or stream channel settings similar to those described above for multiple-carcass Hadza processing sites (compare Figures 4–5), but where the Hadza themselves seldom camp. Given the greater

Table 4 Large animal body part representation at a currently-used Hadza hunting blind *vs.* Plio-Pleistocene sites

	n	Skull	Vertebra	Rib	Scapula/ pelvis	Limb total	Manus/ pes
Hadza hunting blind	442	26	8	13	1	40	12
BK	1444	33	5	11	3	40	8
FxJj 50	739	13	7	38	1	39	3
FxJj 64	107	14	0	73	0	11	3
FLK Zinj	3513	28	5	18	2	42	5
MNK	842	34	7	7	5	36	12

(*n*) is the number of identified specimens (NISP); all other columns are approximate percentages of (*n*). Data on early archaeological sites from Table 1; Hadza hunting blind data from Lupo & O'Connell (2002: Table 1).

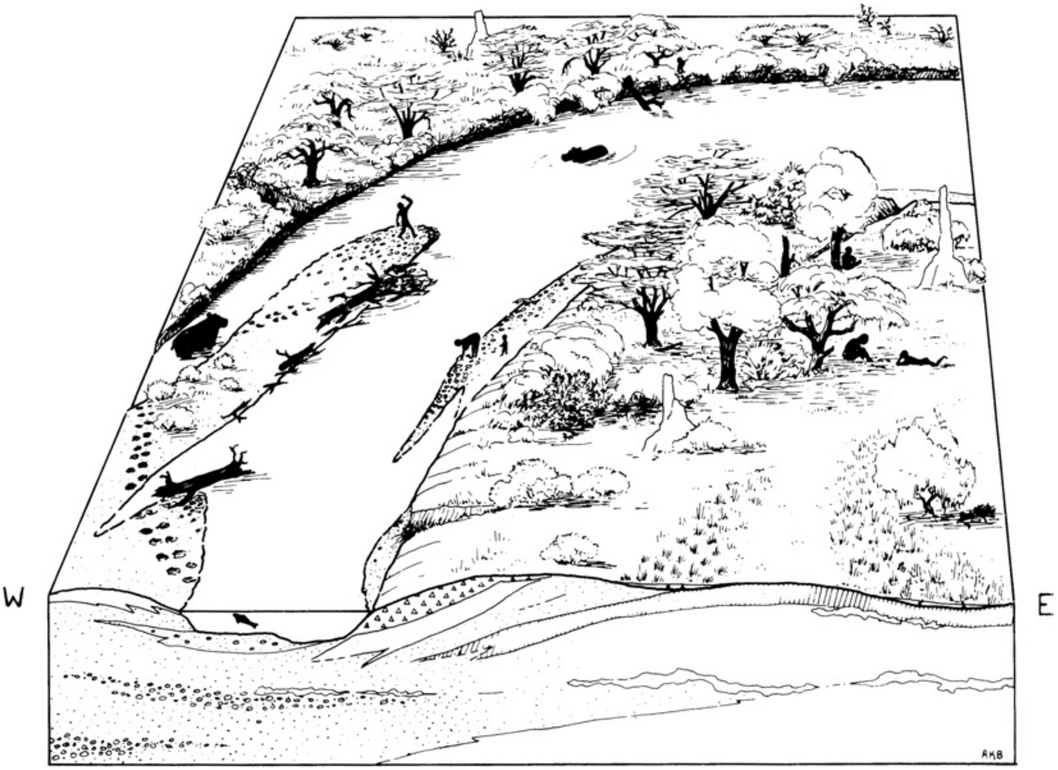

Figure 5. Geomorphologically based reconstruction of Koobi Fora site FxJj 50 at time of early human use (after Bunn *et al.*, 1980 reproduced by permission of Taylor & Francis, Ltd.).

formidability of the Plio-Pleistocene predator guild (see below), it seems highly unlikely that early humans did so either.

- Many include the remains of very large ungulates. More than 25% of total NISP from the seven Koobi Fora localities listed in Table 1 represent animals in size classes 4–6, with adult body weights >300 kg. If transport economics were similar to those in the modern Hadza case (Figure 3), these animals were almost certainly acquired close by, probably within 100–200 m of the point at which their bones were ultimately deposited.

- Most have yielded assemblages dominated by head and limb parts, a pattern nearly identical to that seen in Hadza near-kill accumulation sites (Table 4).

We are leery of making too much of the last point, given that Hadza carcass processing and transport decisions are determined in part by the availability of boiling technology (O'Connell *et al.*, 1990). But on the basis of site location and species representation alone, most of the sites in Table 1 appear to be near-kill accumulation points, *not* home bases. Body part representation patterns are consistent with hominin transport of variable, sometimes broad arrays of elements from nearby kills and subsequent density-dependent attrition by secondary consumers and other non hominin agents. If early hominins did indeed move parts of large carcasses to more distant sites to share with others, archaeological evidence of the practice has yet to be discovered.[5]

Frequency of access

The frequency with which large carcasses were acquired can be assessed in two ways. The first is based on estimates of the time periods over which large animal bone assemblages were accumulated. Combined with data on numbers of individual animals (MNI) represented, these estimates can be used to calculate carcass acquisition rates.

The shortest time estimates resulting from this approach are those offered by Bunn (1986, 1997), who reckons that some assemblages (e.g., FLK Zinj, FxJj 50, FLKN 1/2) were laid down in less than a year. For FLK Zinj and FLKN 1/2, where MNI estimates are as high as 45–50 (Table 1), this implies *minimum* acquisition rates approaching one large animal (or parts thereof) per week. Given that MNI counts have almost certainly been reduced by post-depositional attrition, *and* that early hominins deposited large animal bones at more than one site in the course of a single year, the overall acquisition rates implied are quite substantial.

The problem with this particular calculation lies in Bunn's time estimates, which are based on the degree of weathering damage displayed by the bones in each assemblage, compared with a control schedule for bone exposed on the ground surface in similar habitats today (Behrensmeyer, 1978). Many have observed that Bunn's estimates are unlikely to be reliable, mainly because the control schedule was calculated on bones exposed to direct sunlight (e.g., Potts, 1986; Lyman & Fox, 1989). Where such exposure is reduced (e.g., by shade or even a light coating of sediment), as was probably the case at these early sites, weathering proceeds more slowly. Bunn's estimate does not control for this complication. Other accumulation rate estimates, based primarily on geomorphological criteria, are much lower. Potts (1986) suggests a minimum of 5–10 years for most sites; Kroll (1994) several decades; Blumenschine and Masao (1991) more than a century; Stern (1993) at least a millennium. Any estimate longer than a decade makes the inferred carcass acquisition rates meaninglessly low.

The second approach involves calculating large carcass acquisition rates for modern hunter-gatherers, identifying their determinants, and assessing their implications for rates that might have been enjoyed by earlier hominins. Once again, some of the best comparative data come from the Hadza (see

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[5] Of the eleven early Pleistocene sites for which detailed data on body part representation are available (Table 2), two fail to fit the head-and-limb dominant pattern found at the other nine. One (GaJi 5) has an unusually high number of pelves; the other (FLKN 6) relatively high numbers of vertebrae and feet. Neither pattern is predicted by current models of large animal bone assemblage formation, including those associated with ethnographically known central place foragers; nor are they anticipated as a result of density-dependent attrition.

also Schaller & Lowther, 1969; Shipman, 1986; Blumenschine, 1987; Turner, 1988; Tunnell, 1990; Tappen, 2001). Since our assessment of the archaeological data suggests that hominins at Olduvai and Koobi Fora acquired large carcasses primarily by aggressive scavenging, we focus on the returns Hadza gain from this activity in particular.

Carcass encounter rates. Pertinent observations were made over a total of 322 days during the years 1985–89 (Bunn *et al.*, 1988; O'Connell *et al.*, 1988*a*,*b*, 1990), in an area that receives about 300–400 mm of rainfall annually (Schultz, 1971). Aerial surveys in the late 1970s indicated large animal biomass values in the 1000–2000 kg/km^2 range, depending on the season (Smith, 1980). These values compare favorably with those reported in game parks and reserves elsewhere in East Africa where rainfall and soil characteristics are similar (East, 1984; Owen-Smith, 1999). We assume that they remained roughly constant through the 1985–89 study period. As indicated above, members of the study population monitored and pursued all scavenging opportunities indicated by circling birds or predator calls. Monitoring for each local group (25–50 people) covered a radius of 10–15 km, roughly 200–500 km^2 total. A total of 20 scavenging opportunities were identified during the study period, an overall average of one every 16 days. Encounter rates were higher in the dry season than in the wet, coincident with higher dry season biomass, related to the presence of perennial water sources. Adjusting for the fact that we have more dry season observation days than wet, we estimate the overall average encounter rate at 20–25 carcasses annually, or about one every 2–3 weeks.

Rainfall estimates for Koobi Fora at the time the early assemblages there were accumulating are in the same range as those for modern Hadza country (Bonnefille, 1976, 1995; Feibel *et al.*, 1991; Wynn & Feibel, 1995), which implies similar large animal biomass values and similar scavenging opportunity rates, roughly one every 2–3 weeks, on average. At Olduvai, rainfall was evidently much higher (800–1000 mm annually), indicating a large animal biomass as high as 10–12,000 kg/km^2 (e.g., Kappelmann, 1984; Cerling, 1992; Sikes, 1994; Reed, 1997; Fernandez-Jalvo *et al.*, 1998; Owen-Smith, 1999). Given a similar monitoring radius (10–15 km), this implies an average scavenging opportunity rate of one every 2–3 days.

Several factors suggest that large animal biomass values and related carcass encounter rates may have been higher in Plio-Pleistocene times, relative to annual rainfall, than estimates based on modern analogues would indicate. Among these are somewhat lower rainfall seasonality (e.g., Cerling, 1992), a more diverse large carnivore guild (see below), and at Koobi Fora in particular the presence of well-watered habitats along the nearby ancestral Omo River (Bonnefille, 1976, 1995; Feibel *et al.*, 1991; Isaac & Behrensmeyer, 1997). Increasing the already high Plio-Pleistocene biomass estimate for Olduvai would have little substantive effect on short term encounter rates, but a similar adjustment for Koobi Fora could well be critical. That said, pollen, paleosol, and other data still indicate a fairly arid habitat away from the Omo River (e.g. Cerling, 1992; Bonnefille, 1995; Wynn & Feibel, 1995), particularly in Upper KBS and Okote times, when several of the sites listed in Table 1 were being formed. This implies low and, in the short term, highly variable carcass encounter rates for the creators of these sites. And if much of the riverine-related large animal biomass were made up of hippopotamids, as data from the archaeological sites lead one to infer (Bunn, 1997), then the increase in predicted encounter rates from this source should have been relatively minor.

Carcass acquisition rates. Hominin capacities for capitalizing on scavenging opportunities depended on their abilities at interference competition. If these were limited, the chances of gaining significant amounts of edible tissue from scavenged carcasses would have been very low, *whatever the potential encounter rate*. Blumenschine (1986) shows that, unless they are interrupted, various East African carnivores, acting in sequence, either completely consume most of their large animal prey, or reduce the edible remains to small amounts of residual flesh and "within-bone nutrients", mainly marrow and brain cavity contents. Our experience in Hadza country is consistent with this observation (see also Bunn *et al*., 1988). For size class 3 and smaller animals (mean adult weights <200 kg), these remnant bits generally represent no more than about 5000 kcal, often much less (Blumenschine, 1991*b*; Blumenschine & Madrigal, 1993; Lupo, 1998). Substantial quantities of flesh are abandoned on only the largest, least often encountered prey (size classes 5–6; mean adult weights >900 kg) (Blumenschine, 1986).

All but one of the scavenging opportunities identified by the Hadza during the study period were created by large predators: hyenas, leopards, and lions. [The exception, a sub-adult elephant, was speared by local pastoralists (O'Connell *et al*., 1988*a*).] In 18 of the other 19 cases, these initial predators were still present when Hadza arrived on the scene. In all 18 cases, Hadza drove them off immediately. Their ability to do so was largely a function of their use of heavy bows, capable of delivering a killing or seriously disabling blow to animals as large as lions at distances of up to 40 m (Bartram, 1997). Without similarly effective weapons, it is unlikely that Hadza would have done nearly so well per encounter, especially against lions, which were responsible for most of the kills they seized.

Comparisons with other modern data are instructive here. Bushmen, for example, are reportedly much less aggressive than the Hadza when presented with confrontational scavenging opportunities (Blurton Jones & Konner, 1976; Lee, 1979; Bartram, 1997; H. Harpending, P. Wiessner, personal communications 2001). This is partly because they use much lighter bows; partly because low ungulate biomass makes successful predators less ready to surrender any prey they succeed in taking. Bushmen also suffer more from direct predation by lions and leopards than do the Hadza (Blurton Jones, Wiessner; unpublished mortality data). Appreciation of the dangers associated with aggressive scavenging is further reinforced by the results of a recent survey of Uganda Game Department records, showing significant numbers of deaths and serious injuries among humans attempting to seize carcasses from large predators, including lions and leopards (Treves & Naughton-Treves, 1999). (See also van Valkenburgh, 2001, on interspecific predation as a cause of mortality among large carnivores.)

As with the Hadza, the great majority of scavenging opportunities potentially available to Plio-Pleistocene hominins were probably created by large carnivores, including lions, leopards, spotted hyenas, the now extinct hyenids, *Chasmaporthetes* and *Pachycrocuta*, and the several machairodont cats, *Homotherium*, *Megantereon*, and *Dinofelis* (Blumenschine, 1986; Marean, 1989; Lewis, 1997; van Valkenburgh, 2001). Their large body size and, in some cases, highly social behavior would have made these predators very dangerous adversaries in aggressive scavenging situations. From an early hominin perspective, the best bets for success may have involved encounters in relatively closed woodland. In these habitats today, lions and leopards are occasionally found alone or in pairs on captured prey, sometimes over periods of several days (Blumenschine, 1986;

O'Connell *et al.*, 1988*a*, 1990; Dominguez-Rodrigo, 1999*a*, 2001). This should have been true in the distant past as well. Machairodont kills may have offered similar opportunities (Marean, 1989; Marean & Ehrhardt, 1995; Lewis, 1997; Turner & Anton, 1997). Hominins might have been able to displace the original predator in some of these situations, particularly if they had the advantage in numbers (e.g., Eaton, 1979; van Valkenburgh, 2001), and if the predator had already fed on the carcass for some time.

The availability and effectiveness of projectile weapons would have been crucial to the resolution of these contests. As indicated above, bows do not appear until the late Upper Pleistocene. Spears or lances would have been useful against predators at very close quarters (e.g., Churchill, 1993); but again the earliest known examples date to the late Middle Pleistocene, more than a million years after the time period of interest. Their absence from the earlier record could well be a function of preservation; but if so, we might still expect indirect indications of their use in both hunting and scavenging situations. The fact that the earliest good evidence of big game hunting roughly coincides with the first direct evidence of spears (Stiner, 2002*a*) suggests that the latter were in fact unavailable to earlier hominins. This leaves us with stone-throwing or perhaps club-wielding as the only remaining options. While these may have been effective at driving off the initial predators in some cases, they are unlikely to have done so nearly as consistently as the bow and arrow do among the Hadza.

If, as in the Hadza situation, scavenging opportunities repeatedly occurred near water points, *and* if early hominins were able to take advantage of them even occasionally, then over decades or centuries sizable faunal accumulations like those in Table 1 could well have developed. But unless those hominins were *at least* as effective as the Hadza at interference competition, meat from large game cannot have been an important day-to-day food source for them except in unusual circumstances. In situations like Koobi Fora in particular, low mean carcass encounter rates and high variance in both the frequency of acquisition and in the size and completeness of carcasses acquired would have made this unlikely.

Discussion

According to the hunting hypothesis, the evolution of early *Homo* was prompted by a climate-driven change in ancestral hominin foraging strategies. Males began to take big game and feed their children, practices that in turn favored increased intelligence, larger brains, delayed maturity, nuclear families, and a sexual division of labor. As recently as the mid-1970s, archaeological data were seen to provide strong support: evidence of big game hunting, the transport of meat to home bases, and the earliest fossil humans were all thought to appear at about the same time, roughly 2 Ma. Despite later challenges to both data and interpretations, this model is still widely favored.

Having reviewed the key aspects of the archaeology, we are now in a position to reassess the basic hypothesis. Three questions are especially pertinent:

- Did early humans hunt large animals and carry the meat to home bases to share with others?
- If not, and if scavenging and near-kill consumption are evident instead, could these practices account for the evolution of early *Homo*?
- If not, how do we explain the coincidence between the earliest dates for *Homo* and the first appearance of sizeable, human-accumulated large animal bone assemblages?

Hunting and home bases

Big game hunting and central place foraging, as evidenced by projectile weapons, damage patterns on ungulate limb bones consistent with early human (but not carnivore) access, and the selective transport of large animal body parts to relatively distant locations, are clearly indicated for the late Middle and early Upper Pleistocene of Africa and Eurasia (50–500 ka, but mainly <250 ka) (e.g., Grayson & Delpech, 1994; Milo, 1994, 1998; Stiner, 1994; Gaudzinski, 1995; Klein & Cruz-Uribe, 1996; Shea, 1997; Theime, 1997; Marean & Kim, 1998; Speth & Tchernov, 1998; Bartram & Marean, 1999; Boeda *et al.*, 1999; Gaudzinski & Turner, 1999; Bar-Yosef & Pilbeam, 2000; Marean *et al.*, 2000; Kuhn & Stiner, 2001; see McBrearty & Brooks, 2000; Stiner, 2002*a* for comprehensive review). Heavy reliance on meat in at least some human populations is further implied by the initial colonization of higher-latitude western Eurasia, probably after 500 ka (Roebroeks & van Kolfschoten, 1995; Kuhn & Stiner, 2001; Stiner, 2002*a*). Stable isotope analysis of Neanderthal skeletal remains provides support for this inference (e.g., Richards *et al.*, 2000; Boucherens *et al.*, 2001). Humans almost certainly could not survive at these latitudes without regular access to meat, probably from big game, at least during the winter months (e.g., Lee, 1968; Binford, 2001).

By contrast, assemblages dated >500 ka show no clear evidence of either big game hunting or central place foraging (Stiner, 2002a). In the best known, most comprehensively-reported set, the 16 Plio-Pleistocene and early Pleistocene sites from Olduvai, Peninj, and Koobi Fora reviewed above, data on site location, prey body part representation, and damage morphology are all more consistent with opportunistic scavenging on kills made by large non human predators. Meat and marrow acquired as a result were probably eaten at or very near the point of initial acquisition. The absence of evidence for projectile weapons might reflect problems of preservation; but if they were in fact available they were evidently less effective than the spears or javelins that appear coincident with other definite indicators of hunting after 500 ka. The lack of evidence for home bases and the long-distance transport of large animal body parts might also be related to problems in discovery, but other aspects of the record argue strongly against it. Consistent early access to large carcasses at a scale likely to generate returns worth transporting is simply not apparent. In short, the material record for early *Homo* is inconsistent with either "hunting" or "home bases" as these terms are customarily understood.

Scavenging and early Homo

Though it does not indicate big game hunting, the pre-500 ka archaeological record does show hominin exploitation of large animal carcasses as early as 2·5 Ma (de Heinzelin *et al.*, 1999), and a sharp increase in evidence for the practice after 1·9 Ma (Potts, 1988; Kibunjia, 1994; Isaac, 1997). The broad coincidence with the earliest dates for *Homo* invites an argument about causal relationships. The question is whether a modified version of the hunting hypothesis, one that appealed to greater access to meat from scavenged carcasses, might explain the complex of traits that distinguished *H. ergaster* from earlier hominins. As indicated above, the traits in question include (but are not limited to) larger body size, later age at maturity, and a greatly increased geographical range.[6]

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[6] Dean *et al.* (2001) present dental micromorphology data indicating that *H. ergaster* and the habilines matured at about the same rate, similar to that seen in modern chimpanzees, and that non habiline australopiths reached maturity even more rapidly (see also Smith *et al.*, 1995). These data are at odds with a much larger body of evidence indicating that australopith (including habiline) and chimpanzee life histories are essentially identical, and that *H. ergaster* matured more

Those responsible for developing the scavenging model have for the most part been silent about such issues (e.g., Blumenschine, 1986, 1991*b*, 1995; Blumenschine *et al.* 1994; Selvaggio, 1994; Capaldo, 1997). Marean (1989) and Potts (1996:124–129) are exceptions. Both contend that Plio-Pleistocene habitat change forced ancestral hominins into more frequent contests with large carnivores, favoring a significant increase in hominin body size. Potts suggests that this in turn favored later age at maturity and the ability to operate in a broader range of environments.

While we agree that the archaeological evidence suggests a pattern of aggressive scavenging on the part of early humans, there are at least two good reasons to reject the argument that this promoted larger human body size and delayed maturation. First, like the hunting hypothesis, this argument assumes that meat from big game was a key component of early human diets, regularly available in quantities large enough to maintain a bigger body and also underwrite the extended pattern of juvenile dependence with which many think it was associated (e.g., Washburn & Devore, 1961; Lancaster & Lancaster, 1983; Hawkes *et al.*, 1998; Kaplan *et al.*, 2000). Daily access to meat in at least some seasons is almost certainly implied, but our analysis indicates that large carcasses could not have been acquired with anything like this degree of frequency and regularity except in unusually rich habitats (e.g., Olduvai). At Koobi Fora, we estimate that early humans encountered scavengeable carcasses at a rate of only one or two a month, and that they actually gained control of the remains, sometimes in a significantly ravaged state, in just a fraction of those cases, say once a month or less. Given the wide range of habitats exploited after 1·8 Ma, acquisition rates this low were probably not unusual for early humans. The consumption requirements implied by the Marean/Potts argument could not have been met under these circumstances.

This problem would have been exacerbated if, as many proponents of the scavenging hypothesis assume, meat were especially important to early humans in the late dry season, when other resources were relatively limited (e.g., Blumenschine, 1986). Large herbivores are often in poor condition at this time of year; and, as Speth (1987, 1989) has shown, humans eating them are likely to sustain a net nutritional deficit as a result. Data from the Hadza underline this point: despite acquiring more than 30 large-bodied prey over a period of 47 days in the late dry season of 1985, the 50-odd members of our study group on average *lost* weight during that period (Hawkes *et al.*, 1991, 1995, 1997), presumably because at least some of the animals they took were in marginal condition. Without access to other resources, mainly underground plant storage organs, they would not have been able to operate in that habitat at that time, the very high rate of carcass access, representing an average of *>1 kg of meat/consumer-day*, notwithstanding (Hawkes *et al.*, 1995, 1997). In other dry seasons in our sample, when large carcass acquisition rates were lower, this pattern of weight loss is absent (Hawkes *et al.*, 1997), probably because consumers were eating less lean meat. Though Plio-Pleistocene seasonality patterns were less extreme than those of today, they were still well defined, particularly after 1·7 Ma (e.g., Cerling, 1992; deMenocal, 1995).

slowly, perhaps at the same rate as do modern humans (e.g., Bromage & Dean, 1985; Beynon & Wood, 1987; Bromage, 1987; Dean, 1987*a*,*b*, 1995; Beynon & Dean, 1988; Conroy & Vannier, 1991*a*,*b*; Smith 1991, 1993, 1994*a*,*b*; Dean *et al.*, 1993; Anemone, 1995; Conroy & Kuykendall, 1995; Clegg & Aiello, 1999; Tardieu, 1998; Moggi-Cecchi, 2001; Anton, 2002; Berge, 2002; see Dean, 2000 for review). The discrepancy is important, but we cannot resolve it here. We emphasize, however, that no matter which model is accurate, significant differences in life history clearly distinguish *H. ergaster* from most (if not all) other Pliocene and early Pleistocene hominins. The emergence of these differences still coincides with an increase in archaeological evidence of meat eating.

The second reason to reject the Marean/Potts argument turns on an appeal to current life history theory. As indicated above, this argument holds that increased competition with predators favored larger body size and, by extension (in Potts' formulation), a delay in age at maturity. The proposed increase in competition almost certainly entailed a greater risk of adult mortality (Endler, 1986; Abrams & Rowe, 1996; van Valkenburgh, 2001). Thus, the argument implies that selection favored later maturity *in tandem with* higher adult mortality rates.

Data from a broad range of taxa and the theory built to account for them in fact indicate just the opposite: age at maturity generally varies *inversely* with adult mortality (e.g., Harvey & Read, 1988; Harvey *et al.*, 1989; Kozlowski, 1992; Charnov, 1991, 1993, 2001; Charnov & Berrigan, 1991, 1993; Hawkes *et al.*, 1998). Juveniles approaching maturity face the trade-off between: (1) the benefits of delaying reproduction in order to grow larger, and so having more production to devote to offspring; and (2) the risk of dying before reproducing. The higher the adult mortality rate, the greater the cost of delay. Models of this sort assume that adult body size is not itself a target of selection, but is instead a function of the age at which growth stops in anticipation of first birth. Theory built to account for broad mammalian (including primate) regularities proposes that adult mortality rates determine age at maturity which, in turn, determines adult body size (Charnov, 1991, 1993, 2001). All else being equal, higher rates of interspecific predation should favor an earlier age at maturity, not a later one.

Critics might well argue that our rejection of the potential role of scavenging in the evolution of *H. ergaster* is flawed on both of the points we cite: (1) large animal prey might have been acquired more often and more reliably than we suggest—say, as a function of generally higher ungulate biomass and related carcass encounter rates than those we proposed above; (2) adult mortality need not necessarily have increased as a function of more intense conflict with large predators. But even if we grant both objections, simply adding more food to juvenile hominin diets should have had the same effect as it does among captive populations of nonhuman primates or human children living in industrial societies (e.g., Altmann *et al.*, 1981; Eveleth & Tanner, 1990). They should have grown faster and reached sexual maturity *earlier*, precisely the *opposite* of the pattern evident in *H. ergaster*.

Accounting for the large animal bone assemblages

This leaves us with the problems posed by the emergence of a zooarchaeological record at about 2·5 Ma, and its increased size and visibility after 1·9 Ma. If, as we contend, this record is primarily the product of hominin scavenging, it is unlikely to reflect a regular feeding strategy, let alone one aimed at provisioning offspring. The dangers associated with pursuing it and the unpredictability of its returns make both readings unlikely. But these same correlates and the desirability of the meat occasionally captured are reasons to favor a very different explanation for this aspect of the archaeology, one that appeals to the importance of male status rivalry among primates in general, and to the "display" functions of hunting and meat sharing in chimpanzees and modern humans in particular.

Over the past three or four decades, observers at various study sites have accumulated a large body of information on hunting among chimpanzees (see Stanford, 1996, 1998; Mitani *et al.*, 2002 for review). Analyses of the context in which this hunting is undertaken, the time devoted to it, and the nutritional returns gained as a result all indicate a practice pursued less for its food value to the hunter than for the advantages it confers in relationships with potential allies and competitors (Nishida *et al.*, 1992; Mitani & Watts, 2001). Male chimpanzees hunt to maintain and enhance their rank in the local group. Status gained as a result has fitness-related advantages, especially in disputes with rivals, notably (but not exclusively) over sexual access to females (Mitani & Watts, 2001). Elsewhere, we have argued that big game hunting often plays a similar role in status competition among modern human foragers (Hawkes *et al.*, 1991, 2001*a*; Hawkes, 1993). Costly signaling models (Zahavi & Zahavi, 1997) promise to explain many aspects of these and other social strategies in both species (Bliege Bird *et al.*, 2001; Hawkes & Bliege Bird, 2002)

One element of chimpanzee hunting involves the "pirating" of kills made by other predators (Morris & Goodall, 1977; Hasegawa *et al.*, 1983; Hiraiwa-Hasegawa *et al.*, 1986; Nishida, 1994; Muller *et al.*, 1995). Though it is often said that chimpanzees do not scavenge, meaning that they do not usually consume the meat of unattended carcasses, this "piracy" is much like the aggressive scavenging reported for the Hadza and other modern hunter-gatherers, the major difference being the size of prey involved. Chimpanzees hunt and "pirate" prey much smaller than themselves; humans in general take a far broader array, including some that are very large.

It seems reasonable to think that the chimpanzee pattern, or something much like it, was also characteristic of australopiths, probably from the time the lineage first appeared, sometime before 4 Ma (Leakey *et al.*, 1994; White *et al.*, 1994). Specifically, we suggest that small game hunting and the occasional seizure of partly consumed carcasses from other predators were normal components of their behavioral repertoire. Results of recent stable isotope analyses of *A. africanus* and *A.* (*Paranthropus*) *robustus*, involving specimens ranging from 1·7–3·0 Ma in age, offer partial support for this proposition: these australopiths evidently ate meat in amounts large enough to affect their skeletal chemistry (Sillen, 1992; Lee-Thorp *et al.*, 1994, 2000; Sillen *et al.*, 1995; Sponheimer & Lee-Thorp, 1999). Carcass acquisition and processing may or may not have involved the use of stone tools. The chimpanzee analogy suggests it did not: the prey involved were probably small enough to be caught and torn apart by hand. Either way, the practice is likely to be difficult, if not impossible to track archaeologically (Plummer & Stanford, 2000; Mercader *et al.*, 2002).

Increased aridity and seasonality beginning 2·5–2·8 Ma (e.g., deMenocal, 1995; Vrba *et al.*, 1995; Bromage & Schrenk, 1999; Marlow *et al.*, 2000; Bobe *et al.*, 2002) should have modified australopith foraging practices and their potential archaeological consequences in several important ways. Greater environmental patchiness, both temporal and spatial, probably limited the availability of formerly important food sources, particularly plants, especially in the dry season (Foley, 1987). Australopiths should have responded by broadening their diets, increasing the array of resources exploited, and devoting more time and effort to processing relative to search (MacArthur & Pianka, 1966). Innovations in processing technology would have been among the predictable results (Hawkes & O'Connell, 1992; Bright *et al.*, 2002). The combination of increased environmental patchiness, broader diet, and related developments in technology, specifically those involving the use of stone, should have combined to produce a (more) visible archaeological signature (see also Sept, 1992*a*).

H. ergaster appeared by 1·7 Ma, possibly as early as 1·9 Ma or before, probably (as we have argued elsewhere) in response to climate-driven changes in ancestral *female* foraging and food sharing practices (Hawkes *et al.*, 1998; O'Connell *et al.*, 1999). The resources involved were probably plants: stable isotope data indicate no difference in degree of reliance on meat by *H. ergaster* relative to the long-standing australopithecine pattern (e.g., Lee-Thorp *et al.*, 2000). Nevertheless, *H. ergaster*'s larger body size should have given it greater competitive ability in contests over carcasses taken by other predators, including some they previously had not dared to engage.

Consider the following scenario. As in East Africa today, carnivore calls and circling birds would have alerted early humans to the death of a large ungulate in the neighborhood. Many would have been drawn to the scene, anticipating the chance to eat meat. But displacing the initial predators would have been difficult. Modern Hadza (men, women and children included) react to these opportunities with great alacrity, confident that that the armed hunters among them will quickly eliminate the competition. For early humans, the absence (or limited nature) of projectile weaponry and potential presence of more and larger predators would have made the odds less favorable and the exercise itself more dangerous. But that very danger and the presence of a large audience would also have created a sometimes irresistible opportunity for males to display their qualities as desirable allies and dangerous competitors. Depending on the size, number and hunger of the carnivores present, the size of the carcass, the amount of meat already consumed, and the size and composition of the assembled human group, the contest may well have been protracted. Rock-throwing and/or stick-wielding advances would have allowed males to distinguish themselves in a very public manner (Kortlandt, 1980). Where success was achieved, both actors and audience probably joined in consuming the prize, either right on the spot or in some shaded area nearby. Increased archaeological evidence of carnivory, particularly involving large-bodied prey, would have been among the results. To the degree scavenging opportunities were differentially and redundantly associated with certain points on the landscape, as they would have been in increasingly patchy Plio-Pleistocene habitats and as they are in Hadza country today, such evidence would become that much more apparent. The sharp trend toward still greater aridity, seasonality and patchiness after 1·7–1·8 Ma (e.g., deMenocal, 1995; Reed, 1997) should have made that record even more prominent, *even in the absence of any real change in degree of reliance on meat.*

As we have assessed it above, the archaeological record is generally consistent with these predictions:

- no evidence of meat eating (other than the stable isotope chemistry) or the use of readily identifiable stone tools prior to 2·5–2·8 Ma;
- limited evidence of both in the 0·5–1·0 Ma period thereafter (e.g., Kibunjia, 1994; Kimbel *et al.*, 1996; Heinzelin *et al.*, 1999; Semaw, 2000; but see Plummer *et al.*, 1999);
- a sharp increase in evidence of large carcass exploitation roughly coincident with the emergence of *H. ergaster* (Potts, 1988; Wood, 1992; Isaac, 1997); some of it associated with patterns in bone damage morphology indicating early carcass access on the part of both humans and large carnivores; most (perhaps all) of it in locations especially suitable for dry season ambush hunting by those same carnivores and, by extension, for competitive scavenging on the part of early humans;
- another "jump" in archaeological visibility, this time involving the appearance of sites in a broader range of habitats (not discussed above, but see Rogers *et al.*, 1994 for details) after 1·7 Ma.

Predictions about both human and related carnivore behavior and their archaeological consequences could be further elaborated, but enough is already in hand to make the beginning of a theoretically and empirically well-supported case. Changes in the early archaeological record of carnivory tell us *not* about the development of paternal provisioning and nuclear families in early *Homo*, but instead reflect the operation of two related processes: (1) a climate-driven change in environment that made the archaeological record of meat-eating more visible; (2) an increase in body size, also climate-driven, that enabled early humans to capture a broader range of prey, mainly via competitive scavenging. The important implication: increased archaeological evidence of meat eating in the Plio-Pleistocene is a *consequence* of the evolution of the *H. ergaster*, not an index of its cause.

Conclusions

The strength of the original Washburn–Isaac argument was its capacity to integrate what was then known about primate and human hunter-gatherer behavior and the fossil and archaeological records in a comprehensive, partially testable model of early human evolution. Over the past 25 years, this synthesis has effectively collapsed, partly because of new discoveries, partly because of changes in related theory and methods.

Nowhere is this clearer than with respect to the archaeology. Actualistic research shows that the record reflects the operation of many processes, both human and non-human. It also shows that the human-related elements are inconsistent with modern hunter-gatherer patterns of settlement and subsistence. Support for contingent inferences about big game hunting, home bases, nuclear families and paternal provisioning—all key elements of the Washburn–Isaac model—disappears accordingly. The prospect that early human behavior differed greatly from that of moderns is strongly highlighted. New ideas about the general shape of that behavior and its evolutionary implications are clearly in order.

So far, however, this challenge has not been met, mainly because most current arguments lack the synthetic breadth of the original formulation. Archaeologists have focused almost exclusively on developing better-warranted models of site formation, giving special attention to the non human forces involved in the process, and for the most part avoiding any reference to hunter-gatherer ethnography or primate ethology. Resulting "bottom-up" inferences about the behavior of early humans are inevitably limited, and without exception fail to address the evolutionary problems now posed by the fossil record (O'Connell, 1995). Those further from the archaeology make the opposite mistake, projecting a model of recent human behavior that is itself under challenge deep into the past, and appealing to an outdated, superficial reading of assemblage composition to support it. This approach ignores the most important result of the actualistic critique, *the demonstration that early humans were behaviorally unlike moderns*. If paleolithic archaeologists now give too much attention to stones and bones alone, those further away give them not nearly enough.

What is required to resolve this impasse is a return to the same synthetic approach that made the Washburn–Isaac model so appealing, and in a scientific sense so effective. The key problems in the Plio-Pleistocene are the shifts in early human diet, body size and life history, the marked increase in geographical range, and the changes in behavior indicated by the large animal bone assemblages. Attention to the similarities we share with other living primates, the differences that distinguish us, and the factors responsible for both provides a basis for attacking these issues. Knowledge of systematic variation in primate life history and its underlying causes has already prompted an hypothesis about the evolution of human body size and life history (Hawkes *et al*., 1998, 2002). This, in turn, has stimulated contingent hypotheses about changes in diet and geographical range, none of which involves big game hunting (O'Connell *et al*., 1999).

Variation in predation among living primates, chimpanzees and humans in particular, offers an equally promising foundation for arguments about the large animal bone assemblages. In both chimpanzee and modern human foraging communities, males spend substantial time and effort on the difficult, dangerous and/or skill-intensive task of acquiring prey. Much of this behavior appears to be promoted by status rivalry (Hawkes & Bliege Bird, 2002). The hypothesis that early *Homo* used the scavenging opportunities presented by Pleistocene carnivores as an arena for display flows from this argument. Combined with inferences about changes in past environments, it can account for the archaeological record now documented for the East African Plio-Pleistocene.

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