Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins

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ARTICLE INFO

Article history:
Received 21 February 2010

Keywords:
Uniformitarianism
Bovid mortality profiles
Carcass foraging
Early Homo
FLK 22 Zinjanthropus

ABSTRACT

The world’s first archaeological traces from 2.6 million years ago (Ma) at Gona, in Ethiopia, include sharp-edged cutting tools and cut-marked animal bones, which indicate consumption of skeletal muscle by early hominin butchers. From that point, evidence of hominin meat-eating becomes increasingly more common throughout the Pleistocene archaeological record. Thus, the substantive debate about hominin meat-eating now centers on mode(s) of carcass resource acquisition. Two prominent hypotheses suggest, alternatively, (1) that early Homo hunted ungulate prey by running them to physiological failure and then dispatching them, or (2) that early Homo was relegated to passively scavenging carcass residues abandoned by carnivore predators. Various paleontologically testable predictions can be formulated for both hypotheses. Here we test four predictions concerning age-frequency distributions for boids that contributed carcass remains to the 1.8 Ma. old FLK 22 Zinjanthropus (FLK Zinj, Olduvai Gorge, Tanzania) fauna, which zooarchaeological and taphonomic data indicate was formed predominantly by early Homo. In all but one case, the bovid mortality data from FLK Zinj violate test predictions of the endurance running-hunting and passive scavenging hypotheses. When combined with other taphonomic data, these results falsify both hypotheses, and lead to the hypothesis that early Homo operated successfully as an ambush predator.

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Introduction

A recent, high-profile hypothesis contends that early Homo employed long distance, endurance running (ER) to hunt and scavenge. More particularly, the hypothesis asserts ER was the specific mode of a general type of predation—persistence hunting (PH)—in which ungulate prey is pursued over a long distance until it fails physiologically and can then be easily dispatched by the hunter(s) (Bramble and Lieberman, 2004). In our recent discussion of that hypothesis, we emphasized paleoecological and, specifically, vegetational context as a key determinant of the viability of ER-PH in tracking and hunting prey animals (Pickering and Bunn, 2007). As a contribution to a uniformitarianist database relevant to paleoanthropology, we cited two ethnographic examples from our own empirical research: one from the Kalahari (Botswana), in which sparse vegetation and a sandy substrate provide an ideal setting for successful hunting by Bushmen using skilled tracking and walking (our example) or ER (Bramble and Lieberman’s example from the literature), and one from the Lake Eyasi region of Tanzania, in which much heavier, savanna–bush–woodland vegetation inhibits tracking of wounded prey or any involvement in ER-PH by Hadza foragers.

Notably, the latter context is comparable to the reconstructed savanna–bush–woodland habitats in which early Homo evolved (e.g., Hay, 1976, 1990; Cerling, 1992; Cerling et al., 1988; Reed, 1997; Sikes, 1994). We proposed that an understanding of predator–prey dynamics, as reflected in large ungulate mortality profiles, enables the development of testable hypotheses about ER-PH in early Homo. We then noted that an actual test of ER-PH using the published ungulate mortality profile from FLK 22 Zinjanthropus (FLK Zinj, Olduvai Gorge, Tanzania), the best available assemblage of butchered fossil bones from a Pleistocene context (e.g., Bunn and Kroll, 1986, 1988; Bunn, 2007; Domínguez-Rodrigo et al., 2007a), flatly contradicts the test predictions of the ER-PH hypothesis, falsifying it.

In a response, Lieberman et al. (2007) imagine we practice the “tyranny of ethnography,” but do not comment on the impact of vegetational context on the evolution of tracking skills in early Homo except to assert definitively that early Homo possessed the necessary skills to track. Further, Lieberman et al. are reticent regarding our proposal and testing of ER-PH with mortality data on ungulate prey, and they offer, instead, a claim about the unlikelihood of efficient hunting or scavenging by hominins lacking bows and arrows or stone-tipped spears, except by ER-PH.

We continue to believe, nevertheless, that ungulate mortality data provide a potentially decisive means of testing ER-PH and other current hypotheses about hominin strategies of prey acquisition in the early Pleistocene, and that hominin foraging adaptations are most
appropriately viewed in an ecological context. In this paper, we develop further the application of ungulate mortality data and vegetational context to the ER-PH hypothesis.

In addition, our data provide a relevant test of the well-known passive scavenging hypothesis (e.g., Binford, 1981, 1985, 1988; Blumenschine, 1986, 1987, 1988, 1991, 1995; Blumenschine et al., 1994), which contends Pleistocene hominins enjoyed very limited access to fleshed carcasses. According to this view, even those carcass parts that hominins infrequently secured were already picked-over by carnivores, leaving no appreciable “surplus” resources for hominin scavengers to share. Binford’s argument for passive scavenging was based simply on a rejection of the results of comprehensive taphonomic analysis of skeletal element representation and cut-mark abundance that belied his beliefs on the bone assemblage from FLK Zinj. Blumenschine, in contrast, acknowledged the taphonomic evidence, including the abundance of cut marks on once-meaty long limb bone shafts, but questioned its interpretation by arguing that a perceived abundance of carnivore gnawing on long limb elements indicated that most meat had already been consumed by primary carnivores prior to acquisition of the carcasses by hominins. According to Blumenschine, passive scavenging from defleshed and abandoned lion kills of large bovids and leopard (Pantherus pardus) kills of small bovids would have yielded marrow bones but marginal remnants of meat, without requiring either hunting or aggressive scavenging by hominins.

Additional actualistic and experimental research, however, contradicts the evidence and reasoning underlying the passive scavenging hypothesis in several ways. First, observations of lion (P. leo) kills by Domínguez-Rodrigo (1999) document complete defleshing of midshaft portions of upper long limb elements (i.e., humeri and femora), leaving no meat to remove in the precise anatomical locations where defleshing cut marks are abundant in the FLK Zinj fauna. Second, strong similarities in the anatomical patterning of cut marks on long limb bone shafts from thorough defleshing of fully-fleshed limbs by Hadza foragers and from hominin butchery at FLK Zinj, indicate that hominins at FLK Zinj similarly possessed fully-fleshed limbs and butchered them for significant amounts of meat (Bunn, 2001, 2007). Third, Domínguez-Rodrigo and Barba (2006; Domínguez-Rodrigo et al., 2007a) established that the incidence of carnivore gnaw marks on long limb elements at FLK Zinj is actually far lower than what Blumenschine reported, because biochemical processes damaged bone surfaces and left many marks mistakenly identified as carnivore gnawing by Blumenschine. For expanded discussion of carcass acquisition by early Pleistocene hominins, see reviews by Domínguez-Rodrigo (2002) and by Pickering and Domínguez-Rodrigo (2006).

Predictions and tests of the ER-PH and passive scavenging hypotheses

We test the ER-PH and passive scavenging hypotheses using the bovid mortality data from the ca. 1.8 million year old (Ma) FLK Zinj zooarchaeological assemblage excavated by Mary Leakey (1971) in Bed I at Olduvai Gorge. As discussed above, the FLK Zinj assemblage exhibits the strongest signal of butchery by hominins of any Bed I site, and indeed, any early Pleistocene site, which implicates early Homo as the dominant taphonomic agent in the transport and systematic butchery of large prey animals recovered there (Bunn, 1981, 1982, 1986; Bunn and Kroll, 1986, 1987, 1988; Potts, 1988). From taphonomic analysis of the FLK Zinj assemblage, Bunn reported more than 200 bones with cut marks, abundant hammerstone percussion damage, and an abundance of limbs and mandibles of an estimated 48 large mammals (minimum number of individuals, MNI) represented. More recent taphonomic analyses have refined the evidence and debated its meaning but without changing the fundamental conclusion that early Homo had the dominant role in forming the bone assemblage (Blumenschine, 1995; Bunn, 2001, 2007; Capaldo, 1997; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2007a; Selvaggio, 1998), Bunn and Kroll (1986) reported a catastrophic mortality profile for the larger ungulates from FLK Zinj, but its meaning was left in doubt in deference to Klein’s (1982: 153, 1986: 446–447, 1999: 461) preference for a very young life-history threshold for defining the onset of old age (i.e., 40%–50% of potential ecological longevity [PEL] in African buffalo [Syncerus caffer] and, he argued, other large ungulates as well (Klein, 1978, 1982: 153; Klein and Cruz-Uribe, 1984: 50, 56, 1996: 322)).

Here, bolstered by a new, behaviorally relevant consideration of bovid age classes (summarized here and fully explicated in an accompanying paper; Bunn and Pickering, 2010), we use the FLK Zinj bovid mortality data to test four discrete predictions that emanate from the ER-PH and passive scavenging hypotheses. One prediction for each hypothesis concerns large, size group 3 bovids and one for each hypothesis concerns smaller, size group 1–2 bovids (see Brain (1974, 1981) or Klein (1976) for definitions of bovid size classes, and Bunn (1986; Bunn et al, 1980) for definitions of more inclusive mammal size groups developed from them).

Test prediction 1 (large bovids)

If early Homo used ER-PH to obtain the size 3 bovids at FLK Zinj, then the mortality data should match what cursorial predators of large bovids are known to kill (which, preferentially, is the relatively vulnerable young and old, more than prime adults).

Test prediction 2 (large bovids)

If early Homo passively scavenged from large felids to obtain the size 3 bovids at FLK Zinj, then the FLK Zinj mortality data should match what lions (as the best available modern proxy for large felid predators of size 3 bovids) are known to kill (i.e., a relatively higher percentage of prime adults than cursorial predators such as spotted hyenas [Crocuta crocuta]).

Even though ER-PH and passive scavenging are generally considered less productive and less likely as strategies for acquiring small bovids, test predictions are similar to those for large bovids. Rapid destruction by feeding carnivores (i.e., large felids or hyenas) of entire small carcasses, bones and all, renders passive scavenging for small bovids unlikely, although the possibility that early Homo, as a non-hunter, could have scavenged from abandoned, tree-stored leopard kills, has been proposed (Cavallo and Blumenschine, 1989). For present purposes, test predictions using mortality data as the test can be tailored directly to these scenarios for small bovids.

Test prediction 3 (small bovids)

If early Homo used ER-PH to acquire smaller, size group 1–2 bovids at FLK Zinj, then the FLK Zinj mortality data should match what cursorial predators are known to kill (again, the relatively vulnerable young and old).

Test prediction 4 (small bovids)

If early Homo passively scavenged from tree-stored leopard kills to obtain small bovids at FLK Zinj, then the FLK Zinj mortality data should match what leopards are known to kill (i.e., a non-age-selective, living-structure sample).

Materials and methods

Paleontological samples

In addition to testing the ER-PH and the passive scavenging hypotheses with the bovid mortality data from the FLK Zinj assemblage, we also present comparative paleontological data from
eight other excavated early Pleistocene levels in Tanzania and South Africa. As with FLK Zinj, three of these levels are in Bed I at Olduvai Gorge. But, in contrast to FLK Zinj, FLK North level 1–2 (FLK N 1–2), FLK North North level 2 (FLK NN 2) and FLK North level 6 (FLK N 6) show little or no evidence of anthropogenic input. Leakey (1971) interpreted FLK N 1–2 as a hominin living floor based on her recovery of ~1205 stone artifacts and 3294 taxonomically varied large mammal bones (plus abundant microfauna) from the ~65 cm-thick level at the site. From preliminary taphonomic analysis, Bunn (1982, 1986) tentatively agreed, based on the finding of a few cut-marked specimens but a notable lack of cut marks in anatomical locations where they are common at FLK Zinj (e.g., distal humerus shafts) and a paucity of hammerstone damage or retfitting long limb bone shafts (which are also common at FLK Zinj). A more recent taphonomic analysis reported butchery damage on these bones and interpreted the fauna as anthropogenic in origin, even more so than FLK Zinj (Capaldo, 1998; Blumenschine et al., 2007). In a thorough reanalysis using a more inclusive, current understanding of taphonomic and diagenetic processes, Domínguez-Rodrigo et al. (2007a) demonstrate convincingly that the anthropogenic damage alleged by Capaldo and Blumenschine is, in fact, a product of trampling of the bones by large animals, sediment abrasion, and large carnivore gnawing. While acknowledging the presence of a few bones with actual stone-tool cut marks, Domínguez-Rodrigo et al. (2007a) attribute the fauna predominantly to predation and feeding by large felids.

At FLK NN 2, Leakey (1971) reported a low-density scatter of 481 bones, but no stone artifacts, from a ~30 cm-thick layer of tuff with clayey patches, which she attributed to hyena activity. Bunn (1982, 1986) reported abundant carnivore damage on the bones, plus one specimen with stone-tool cut marks, and generally concurred with Leakey’s interpretation, as did Potts (1988). Reanalysis by Domínguez-Rodrigo et al. (2007a) indicated large felid, rather than hyena, activity as the source of the bones.

At FLK N 6, Leakey (1971) recovered an essentially entire skeleton of an elephant (Elephas recki), 123 stone artifacts, and ~400 bones of other large mammals, from a ~45 cm-thick layer of silty clay. Leakey interpreted the site as an elephant butchery by hominins in a swampy area, a notable conclusion that was at least partially supported by subsequent reports of rare cut marks on a few of the elephant bones (Bunn, 1982, 1986; Potts, 1988). From taphonomic analysis of the non-elephant (mostly bovid) bones, Bunn (1982, 1986) concluded that the fauna was predominantly a non-anthropogenic, natural background, with a bovid MNI of 35, many complete bovid long limb bones (likely biased during excavation against recovery of fragmentary long limb bone shafts), many specimens striated from trampling, and several specimens (bovid long limb elements and a hippopotamus metacarpal that had been misidentified as a rhinoceros) exhibiting probable stone-tool cut marks. Domínguez-Rodrigo et al. (2007a: 110) conclude that all of the linear grooves on elephant and bovid bones (the hippopotamus metacarpal was not located for reexamination) at FLK N 6 “can be best explained as abrasion marks.”

For present purposes, we analyze bovid mortality data from FLK N 1–2, FLK NN 2, and FLK N 6, as samples of probable non-anthropogenic, natural background occurring on the Olduvai paleo-landscape during the Bed I time interval under study. This enables an initial investigation for any resemblances or differences in bovid mortality between these likely natural samples and the predominantly anthropogenic sample from FLK Zinj. We do not regard these data as “controlled,” simply because many of the specific events and processes involved are unknown or unknowable. We view all of these sites as natural history sites, or palimpsests (e.g., Isaac, 1984; Domínguez-Rodrigo et al., 2007a), in which multiple taphonomic agents, including hominins, had varying contributions. For more controlled comparative analysis, we then rely on data from modern wildlife research in which the predation patterns of various large carnivores are known (see below). From the same perspective, we also analyze fossil bovid mortality data from three South African cave sites (five stratigraphic levels), which are inferred predominantly as products of large carnivore predation, although recent taphonomic analyses have established that hominin butchery activities also contributed to site formation in some cases (Brain, 1981, 1993; Watson, 1993a; Pickering et al., 2004a,b, 2005, 2007, 2008; Adams, 2006; Thackeray, 2007). Swartkrans, Kromdraai and Gondolin all formed as phreatic maze-caves in the dolomites of the Chunniespoort Group, probably sometime in the Miocene and only opened to the land surface at various times throughout the Pliocene and Pleistocene, when they were then able to capture and incorporate terrestrial debris into their paleoanthropologically productive breccias. Swartkrans is the best understood of the sites in terms of stratigraphy and has yielded the richest traces of early hominin behavior—including Developed Oldowan/Early Acheulean stone tools, butchered animal bones and bone digging tools—in its three Pleistocene units, Members 1–3 of the Swartkrans Formation; Member 3 also produced bones that were possibly burned in hominin-tended fires (Brain, 1993). While it is important to stress that, overall, hominins contributed only minimally to the ca. 1.0–1.8 Ma faunas from Swartkrans Member 1–3, it is equally important to emphasize that those fossils that were modified by hominins are informative behaviorally: the total butchered sample from each member is comprised of high proportions of meat-bearing upper and intermediate (i.e., radiolunae and tibiae) limb elements, indicating early access to carcasses by hominin foragers (Pickering et al., 2007, 2008) (see preceding discussion).

No hominin fossils have been recovered from Kromdraai A. However, Thackeray et al. (2005) employed X-ray diffraction analysis to detect bone apatite on one of the polyhedral core artifacts discovered at the site (Kuman et al., 1997). Subsequently, Thackeray (2007: 67) elaborated that this finding, combined with the site’s carnivore:ungulate ratios and long limb bone shaft fragment size distribution, indicates that hominins used the Kromdraai A artifacts to “opportunistically...obtain bone marrow from [the site, which was also] used at least temporarily by large carnivores such as saber-tooth cats, which preyed primarily on juvenile alcelaphines.” Large carnivores have long been implicated as primary bone collectors at Kromdraai A (e.g., Brain, 1981). Thackeray’s specific accusation of Dinofelis is based, in part, on its presence in the Kromdraai A fauna (Brain, 1981). Thackeray and his co-workers (Thackeray and Van Leuven Smith, 2001; Lesnik and Thackeray, 2006) argue that the mortality profiles (based on molar crown height measurements) of alcelaphines and Equus show a pattern similar to that created by modern lions: with the old of smaller species and juveniles of larger species preferentially represented. Thackeray and Van Leuven Smith (2001: 11) then cite that “Lewin (1997) has previously suggested that Dinofelis displayed behavior similar to that of modern lions.”

A fossil assemblage excavated by E.S. Vrba and D. Panagos from sediments adhering to the northeastern cave wall of Gondolin does not contain hominin remains or artifacts (Watson, 1993b). More recent excavation of a test trench into an ex situ brecia dump, created by early 20th century lime miners at the site, has yielded the isolated M3 of a robust australopithecine and an isolated M4M3 or M3 of a non-robust hominin (Menter et al., 1999). No stone tools were recovered from the dump excavation, but one of us (TRP) did identify, in the field, an ungulate long limb bone shaft fragment that preserves possible stone-tool cut marks. However, an exhaustively detailed study of the Gondolin faunas (Adams, 2006) supports Watson’s (1993b) earlier conclusion that the bovids from the Vrba–Panagos sample were probably collected and modified exclusively by leopards.

**Paleontological analyses**

Because the Olduvai and South African bovid dental samples are differentially preserved we employed multiple analytical methods.
that best matched the condition of each assemblage. For the Olduvai samples, all excavated dental specimens that could be identified to taxon (species or otherwise unrepresented bovid tribe or size group) were used to determine MNI and age, including partial and complete hemimandibles (most MNIs were based on these), maxillary denticions, and isolated teeth. Tooth eruption sequence, homologous tooth size, and the progressive loss of molar infundibula with advancing age (generally from mesial to distal), were all used in these determinations. In contrast, the bovid samples analyzed from Kromdraai A and Gondolin were restricted to non-antimeric hemimandibles. For each hemimandible, individual teeth were first assigned an eruption/attritional score, and then the specimen as a whole was assigned to an age class (see Bunn and Pickering, 2010). The Swartkrans samples were not available for study so we used Watson’s (1993a) published data on bovid mortality for the site. Even with the inclusion of fragmentary specimens from Olduvai, sample sizes are small, ranging from MNIs of 1–9 per bovid species, whereas the South African samples are larger, ranging from MNIs of 10–27 per bovid species. To achieve usable sample sizes, some analytical pooling of species MNIs into size groups based on estimated live animal weights was employed.

**Modern African bovid samples**

A long history of research and an extensive literature on modern African wildlife provide essential empirical data used in the comparative analyses herein. Long-term, field-based research in some notable ecosystems (e.g., the Serengeti) documents predator–prey dynamics and provides essential, large datasets on the age structure of various bovid populations and on the mortality structure of bovid prey samples from the major carnivore predators involved. Laboratory research on the degree of correlation between ontogenetic age and dental attrition provides data for a representative range of taxa. Unsurprisingly, these many independent projects have developed a range of descriptive systems for defining age categories suited to their particular objectives. Some of this research employs cementum increment analysis in combination with loss of molar infundibula, yielding high-resolution age classes of 1–3 yr. Other studies use dental attrition in incisors, horn development, and changes in body form, which are convenient methods for aging of animals in the field but less applicable in paleontological analyses, based, of necessity, on attrition in the commonest molar teeth.

As in Stiner’s (1990) earlier research on this subject, we made a concerted effort to match the various degrees of temporal resolution and definitions of mortality class boundaries, to ensure that our age classes group fossil and modern animals of the same age range and that those classes are relevant to the hypotheses of hominin meat foraging that are being tested. Our accompanying methodological paper details the theoretical background and development of our categorization system (Bunn and Pickering, 2010), which we summarize here.

**Analytical age and mortality classes for ungulates**

Ungulates enter adulthood when they lose all deciduous teeth and begin to show occlusal wear of all permanent teeth. Prior to adulthood, an individual is considered a juvenile, a major stage of life history that is ~20% of its total lifespan or PEL. We divide the juvenile stage into young juvenile (newborn through yearling) and subadult juvenile substages. Bovids classified as young juveniles possess light to moderately worn deciduous premolars and erupting M1 and sometimes M2. Young juveniles are excluded from our analyses for two reasons. First, young juvenile teeth are usually destroyed when subjected to rigorous biostratinomic and diagenetic forces (e.g., Munson, 2000; Munson and Garniewicz, 2003) and are thus relatively uncommon in paleontological samples compared to modern control samples, in which they are relatively common. Second, hypotheses of hominin hunting discern between “gathering” of weak, slow and naïve baby animals and dispatching older animals that possess adult or near-adult strength, speed and savvy. In contrast to young juveniles, subadult juveniles meet this latter description in physical and behavioral capabilities and we thus restrict analysis of juveniles to this substage, defined dentally by moderately to heavily worn or shed deciduous premolars and erupting permanent premolars and third molars.

We use three categories, early prime, late prime and old, to classify adult animals. Early prime, is from ~20%–50% of PEL (in some studies, this extends to ~60% of PEL); an early prime animal has full permanent dentition showing light to moderate and substantial occlusal wear but

![Figure 1. Fossil bovid dentitions from FLK Zinj illustrating occlusal wear stages for three adult age categories. Specimens D 41 and D 122 are the associated hemimandibles of a prime adult *Kobus sigmoideus*; note the considerable wear on the occlusal surfaces of the teeth, but that all molar infundibula are still intact (a). Specimens D 42 and B 347 are the associated hemimandibles of an old adult (just beyond the late prime-old age threshold) *Parmularius altidens*, which show the recent loss of the mesial infundibula from the M1s (b). Specimens G 294 and D 35 are the associated hemimandibles of an old adult male *Ardiceras reckii*, which show loss of all molar infundibula (c).](image-url)
no loss of molar infundibula (this categorization applies to size group 3 bovids, not to smaller taxa, which start losing lower molar infundibula earlier in life). Late prime is from ~50%–75% of PEL; a late prime animal has moderate and substantial occlusal wear but no loss of mesial infundibulum from M₁; (3) old is from ~75%–100% of PEL; an old animal has heavy occlusal wear and progressive loss of both mesial and distal infundibula from the lower molars M₁ and M₂ (this categorization applies more widely across bovid size groups).

We argue that although some late prime and old animals have passed through a series of discrete life-history events that define them as physiologically past prime, they still retain formidable capabilities to evade and defend against predation. This position, developed fully in our accompanying paper (Bunn and Pickering, 2010), impacts our interpretation of the fossil bovid mortality patterns discussed below. Figure 1 illustrates fossil bovid specimens from FLK Zinj representing the different adult age classes.

Presentation of data

For visual comparison of different mortality samples we followed methodology developed by Stiner (1990), who divided data into juvenile, prime, or old groups, then converted those data to percentages for each sample, and plotted each sample as a discrete point on a triangular graph. To control for differences in sample sizes we used computer software (modified triangular graph program) created by Steele and Weaver (2002) that employs bootstrapping to produce a density contour around each graphed sample point, approximating a 95% confidence interval.

Results

Table 1 shows the mortality data and the broad taxonomic diversity among the fossil bovids from FLK Zinj. To enable comparative analysis, data for the other Pleistocene assemblages from Olduvai and from South Africa, and those for some of the best-documented case studies of modern predator–prey dynamics in the Serengeti ecosystem are also included in Table 1. The obvious disparity in sample sizes between the generally smaller fossil samples and the larger wildlife samples is controlled statistically with the modified triangular graph program of Steele and Weaver (2002), using the mortality data from the different contexts (Table 2).

The introduction to this paper presented four predictions for bovid mortality patterns should the ER-PH hypothesis or passive scavenging hypothesis be true. Our results provide the tests of those predictions. First we consider test implications for large, size group 3 bovids, under each hypothesis. To restate:

Test prediction 1. If early Homo used ER-PH to obtain the size 3 bovids at FLK Zinj, then the mortality data should match what cursorial predators of large bovids are known to kill (which, preferentially, is the relatively vulnerable young and old, more than prime adults).

Test prediction 2. If early Homo passively scavenged from large felids to obtain the size 3 bovids at FLK Zinj, then the FLK Zinj mortality data should match what lions (as the best available modern proxy for large felid predators of size 3 bovids) are known to kill (i.e., closer to an unselective, living-structure prey sample, with a relatively higher

Table 1
Age frequency distributions in African fossil and modern samples of bovid dental remains.a,b

<table>
<thead>
<tr>
<th>Site/predator</th>
<th>Size group</th>
<th>Taxon</th>
<th>MNI</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Young juvenile</td>
</tr>
<tr>
<td>Olduvai FLK Zinj</td>
<td>1</td>
<td>Antidorcas recki</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>Antilopini</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1 and 2</td>
<td>Total</td>
<td>7</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>3a</td>
<td>Parnularius altidens</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>3b</td>
<td>Connochaetes sp.</td>
<td>3</td>
<td>3</td>
<td></td>
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<td>3b</td>
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<td>2</td>
<td>3</td>
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<tr>
<td>3b</td>
<td>Oryx sp.</td>
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<td>1</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Total</td>
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<td>3</td>
</tr>
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<td>4</td>
<td>Syncerus caecilus</td>
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<td></td>
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<td>Total</td>
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<tr>
<td>1 and 2</td>
<td>Total</td>
<td>33</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td>Gondolin</td>
<td>2</td>
<td>Reduca sp.</td>
<td>27</td>
<td>3</td>
</tr>
<tr>
<td>Leopard</td>
<td>1</td>
<td>Gazella thomsoni</td>
<td>30</td>
<td>9</td>
</tr>
<tr>
<td>Lion</td>
<td>1</td>
<td>Gazella thomsoni</td>
<td>204</td>
<td>67</td>
</tr>
<tr>
<td>3b</td>
<td>Connochaetes taurinus</td>
<td>262</td>
<td>72</td>
<td>50</td>
</tr>
<tr>
<td>3b</td>
<td>Kobus ellipsiprymnus</td>
<td>9</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Cheetah</td>
<td>1</td>
<td>Gazella thomsoni</td>
<td>192</td>
<td>124</td>
</tr>
<tr>
<td>Spotted hyena</td>
<td>1</td>
<td>Gazella thomsoni</td>
<td>98</td>
<td>42</td>
</tr>
<tr>
<td>3b</td>
<td>Connochaetes taurinus</td>
<td>86</td>
<td>31</td>
<td>15</td>
</tr>
<tr>
<td>Wild dog</td>
<td>1</td>
<td>Gazella thomsoni</td>
<td>65</td>
<td>34</td>
</tr>
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</table>

a Abbreviations: FLK Zinj = FLK 22 Zinjanthropus; Swartkrans 1 = Swartkrans Member 1; Swartkrans 2 = Swartkrans Member 2; Swartkrans 3 = Swartkrans Member 3; MNI = minimum number of individuals.

b All fossil data except those from Swartkrans (Watson, 1993a) were generated by the authors. See also Bunn and Pickering (2010–this issue) for details of the Gondolin mortality data. Modern wildlife data are from Schaller (1972), Kruuk (1972), and Spinage (1982).

c Site/predator = for fossil assemblage of inferred, but ultimately unknown taphonomic derivation, the site name is provided, in contrast to the predator species that is provided for samples that formed under direct, modern observations.

d Bovid size groups follow Bunn (1986); see text for discussion and additional references.
All fossil data were generated by the authors. Bovid size groups follow Bunn (1986); see which we have assigned to age class based on proportions occurring in Schaller’s gazelle age classes, the second sample includes Schaller’s unaged adults (n=58), prime and old adult Antidorcas recki, which, based on their size and rugosity, are male animals. The mortality distribution of small bovids from FLK Zinj is statistically distinct from and, thus, contradicts the test implications of passively scavenging from leopard or cheetah (Acinonyx jubatus) kills. It is probable, at a 95% confidence level, that the small bovids whose butchered bones were found at FLK Zinj were not acquired by passive scavenging from leopard kills. Small-bovid mortality data from Swartkrans, Kromdraai A, and Gondolin, on the other hand, do support the attribution of those remains to leopard (or another felid ambush predator) kills, which has been argued previously from evidence of prey body size, skeletal part representation and bone damage (e.g., Brain, 1981, 1993; Pickering et al., 2004b, 2007, 2008) (Fig. 5). Similarly, small-bovid mortality data from FLK N 1–2 and from FLK N 6 also exhibit a living-structure pattern that is statistically indistinguishable from leopard prey, which contrasts from FLK Zinj also contradict aggressive, power scavenging from lions, an alternative hypothesis developed, in the absence of evidence of hunting by hominins, to account for the abundance of the very skeletal elements defleshed quickly by lions and the abundance of defleshing cut marks on them. The large bovid mortality data from FLK Zinj correspond to Stiner’s definition of a “primedominated” pattern, which she attributes exclusively to selective hunting by humans (Stiner includes young juveniles, which are excluded here; including young juveniles increases the statistical separation between lion-killed wildebeest [Connochaetes spp.] and size-group 3 bovids at FLK Zinj). To add a comparative perspective, however, the mortality data for large bovids at FLK Zinj also show strong similarity to other Bed 1 Olduvai assemblages in which butchery evidence is uncommon or absent (Fig. 3), which warrants further discussion.

The restated test implications for smaller, size-group 1–2 bovids are:

Test prediction 3. If early Homo used ER-PH to acquire smaller, size group 1–2 bovids at FLK Zinj, then the FLK Zinj mortality data should match what cursorial predators are known to kill (again, the relatively vulnerable young and old).

Test prediction 4. If early Homo passively scavenged from tree-stored leopard kills to obtain small bovids at FLK Zinj, then the FLK Zinj mortality data should match what leopards are known to kill (i.e., a non-age-selective, living-structure sample).

As shown in Figure 4, the small-bovid data from FLK Zinj are dominated by old adult Antidorcas recki, which, based on their size and age, are male animals. The mortality distribution of small bovids from FLK Zinj is statistically distinct from and, thus, contradicts the test implications of passively scavenging from leopard or cheetah (Acinonyx jubatus) kills. It is probable, at a 95% confidence level, that the small bovids whose butchered bones were found at FLK Zinj were not acquired by passive scavenging from leopard kills. Small-bovid mortality data from Swartkrans, Kromdraai A, and Gondolin, on the other hand, do support the attribution of those remains to leopard (or another felid ambush predator) kills, which has been argued previously from evidence of prey body size, skeletal part representation and bone damage (e.g., Brain, 1981, 1993; Pickering et al., 2004b, 2007, 2008) (Fig. 5). Similarly, small-bovid mortality data from FLK N 1–2 and from FLK N 6 also exhibit a living-structure pattern that is statistically indistinguishable from leopard prey, which contrasts...
with earlier reconstructions of FLK N 1–2 as an occupation floor produced by hominins but is consistent with recent attribution of small bovids there as leopard prey based on patterns of skeletal representation and bone damage (Domínguez-Rodrigo et al., 2007a,b; Domínguez-Rodrigo and Pickering, 2010; contra Blumenschine et al., 2007) (Fig. 6). Bovid remains at FLK N 6 have always been considered a natural background, rather than food refuse of hominins; the mortality data on small bovids presented here are consistent with evidence of skeletal representation and bone damage, as reported by Domínguez-Rodrigo et al. (2007a), in specifying leopard predation as a likely dominant factor.

In contrast, the old-male-dominated pattern of A. recki mortality in the FLK Zinj assemblage is not inconsistent with the ER-PH hypothesis. This is the single prediction tested in this study that is met. In that context, we still seriously question the plausibility of ER-PH as a regular carcass acquisition strategy for early hominins, a point we expand upon below.

Discussion

Given the abundance of large-bovid long-limb bone specimens with defleshing cut marks and the quantity of the very skeletal elements eaten first by carnivores at their kills, which implies early access by hominins to intact carcasses (see detailed discussions in Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, 2006), the simple conclusion from the statistically distinct, prime-dominated mortality profile for FLK Zinj is, or could be, that early Homo, as ambush predators, killed the large bovids. The mortality distribution of large bovids from FLK Zinj, however, also shows strong similarity and no statistical separation from the large bovids from FLK N 1–2, FLK NN 2, and FLK N 6. These latter bovid assemblages exhibit little (FLK N 1–2, FLK NN 2) or possibly no (FLK N 6) butchery evidence, and based on bone damage patterns, they have recently been attributed mainly to predation and feeding by large felids (Domínguez-Rodrigo et al., 2007a). It is possible that ambush predation by large felids was dominant in all three of these “background” Olduvai assemblages (and, unsurprisingly, in the Olduvai paleo-community in general), with the wealth of butchery evidence at FLK Zinj reflecting both hunting success by early Homo and access to complete and fairly complete carcasses by power scavenging from felid predators. In any case, the prime-dominated mortality profile for large bovids from FLK Zinj falsifies ER-PH as a credible explanation for the zooarchaeological and taphonomic patterns observed in the assemblage.

Those patterns also argue strongly against passive scavenging by hominins as a significant factor in creating the FLK Zinj large bovid subassemblage. Using mortality data to evaluate this assertion is complicated by the fact that the comparative fossil samples from Olduvai “background” sites (FLK N 1–2, FLK NN 2, FLK N 6) are small and thus the 95% confidence contours for those probable felid-derived assemblages are large. If instead the “background” samples are pooled it emphasizes their more even, living-structure age distribution, in contrast to the prime-dominated pattern at FLK Zinj. The prime-dominated pattern at FLK Zinj also trends away from the living-structure age distribution patterns evident in modern lion kills.

Yet another way to increase sample sizes analytically is to include young juveniles in the comparison of FLK Zinj and the pooled “background” sites, and our subdivision of mortality data into multiple age classes is designed to enable and encourage such flexibility in analytical approach. The presence of relatively fragile,
young juvenile specimens in all of these assemblages argues against severe, density-mediated biasing from biostratigraphic (carnivore scavenging) or diagenetic (profile compaction) processes. At FLK Zinj, for example, in addition to very young juvenile (or fetal) bovids, there are also teeth of a young juvenile suid and hemimandibles of a young juvenile giraffe, and in each of the background assemblages, multiple young juvenile suid individuals are also represented. Figure 7, which includes young juveniles and subadult juveniles in the juvenile class, shifts the distributions toward the juvenile side and shows more clearly the living-structure pattern of the “background sites.” If the young juveniles bovids at FLK Zinj are actually fetal (these deciduous upper premolars are essentially unworn, and Spinage (1967) reports this condition at birth but not at six months of age in modern waterbuck [Kobus ellipsiprymnus]) and excluded (as in Fig. 3) because they were not directly hunted and killed, then there is an even clearer separation between the prime-dominated mortality at FLK Zinj and the living-structure mortality at the “background” sites. This likely indicates a derivation from a different source: ambush hunting by early Homo at FLK Zinj, rather than any form of scavenging from felids or ER-PH. Since the initial writing of this paper, two additional maxillary and mandibular specimens of waterbuck have been identified by HTB in the original fossil assemblage from FLK Zinj. These specimens (catalog numbers B 4 and C [no number, so it was likely recovered from the screen]) represent two additional individuals that died younger than the two fetal or neonatal individuals previously known (as discussed above) and are clearly fetal (unworn upper and lower deciduous premolars). This raises an intriguing possibility in relation to the small prime adult waterbuck individuals (MINI = 7 adults, of which three are smaller, early prime females and four are larger, late prime males) from FLK Zinj: the targeted prey of hominin ambush hunting was likely pregnant or recently pregnant female and somewhat older, perhaps non-territorial male waterbucks.

Even though ER-PH was argued to be most productive for hominins when used against large, size group 3 prey, we reiterate that the old-male-dominated pattern in A. recki mortality at FLK Zinj does not contradict the prediction of the ER-PH hypothesis for small bovids. We question, however, the relative merits and adaptive value of targeting small, old gazelles in their preferred bush–woodland habitat by jogging with eyes fixed to the ground in a most challenging tracking exercise right through the prime hunting habitat of large felids, when the same bovids could have been exploited by Homo as a ambush predator, alert to all animal movements in these relatively vegetated settings.

At the risk of being branded ethnographic tyrants again (and falsely), we recall our empirical observations that small bovids can be walked to exhaustion—not requiring ER—by modern, highly skilled Kua hunters at a significant physical cost to them, in the sparsely vegetated, soft sandy substrate of the Kalahari that is the ideal context for using sophisticated tracking skills. In the more heavily vegetated savanna–bush–woodlands that characterize the East African Rift Valley today, and paleoenvironmental reconstructions of the habitats in which early Homo evolved in the Pleistocene, even greater tracking skills beyond those possessed by modern foragers would be required to succeed at ER hunting. Despite long-term ethnographic research, the Hadza have not been observed either attempting, much less succeeding at ER hunting in the more vegetated East African Rift Valley. This demonstrates a likely cause–effect relationship between vegetation cover and viability of tracking, and it casts doubt on the likelihood of highly sophisticated, successful tracking by early Homo.

This, of course, does not mean that ER-PH never happened in the Pleistocene. It simply illustrates that a different ethnographic example (i.e., hunting with bow-and-arrow) emphasized by Lieberman et al. (2007: 442), when viewed in broader and better-matched ethnographic and ecological perspective, does not provide quite the epiphany about the evolution of ER-PH hunting that is desired: “In fact, without projectiles, it is hard to imagine how early Homo in the [Early Stone Age] would have either scavenged or hunted safely or effectively unless they employed ER to some extent.” Ironically, Lieberman et al. base that claim on their assertion that because of technology, hunting strategies of recent foragers are not useful analogs for early Homo, which they then justify using survey results of ethnographic hunting technology (e.g., spear efficiency). Lieberman et al. confuse and conflate the concepts of hunting efficiency and hunting capability. In all likelihood, hunting efficiency is significantly increased in recent contexts with bows and arrows, relative to the Pleistocene, but it does not follow from relative efficiency, that hunting capability in the absence of bows and arrows was lacking (except by ER).

Logically extending such hyperbole to include actual scientific evidence, would mean that in the vast array of paleoecological contexts in which hunting is reconstructed—from Gona to the most recent hunter missing his bow and arrows, from flat, sandy terrain to steep, wooded, rocky slopes, and from tropical and temperate regions—prehistoric and past human hunting (and scavenging) without bows and arrows reduces to ER (or hopeless inefficiency?). To learn about past human foraging strategies, including all forms of hunting and scavenging, it is not justifiable scientifically to assume and attribute to early Homo, or to their immediate ancestors, the sophisticated tracking skills of modern humans or skills beyond those of modern humans—essential to the success of ER-PH—when the evolution of hunting capabilities is the very topic being investigated.

Rudimentary tracking skills would not enable successful, much less, efficient ER, in the vegetated East African Rift Valley paleoenvironments in which early Homo evolved. And it is not reasonable to assume sophisticated tracking skills in early Homo, while at the same time discounting any intellectual ability to ambush prey. In the absence of direct evidence, we do not know how early Homo would have hunted large prey (sensu Bunn and Kroll (1986)), who for that reason raised the alternative of aggressive, power scavenging; contra Lieberman et al.’s characterization), but there is compelling evidence that Pleistocene Homo had early access to intact, prime adult, large bovids.

A plausible method of ambush hunting would require that hominins had the ability to get close enough to prey animals to inflict a mortal wound and that they had the technology to do so. One likely method of achieving exceedingly close encounters with prey animals that is known to be effective in modern contexts is climbing into a tree
along a game trail and simply waiting for animals to walk by with
their gaze fixed horizontally to guard against terrestrial predators. As
for lethal weaponry, wooden spears are a distinct possibility, although
we emphasize that there is currently no direct evidence of such
technology. We pose three questions: 1. Was there a wood-chopping
function for Oldowan choppers whose edges are battered through use
as tools (e.g., Hayden 2008), comparable to the woodworking
activities reconstructed by Domínguez-Rodrigo et al. (2001) from
wood phytooliths on Acheulean tools at Peninj (Tanzania)? 2. What
was the hominin task that produced microwear evidence of wood
saving or scraping on Oldowan stone flakes at Koobi Fora (Kenya)
(Keeley and Toth 1981)? 3. If a chimpanzee level of cognitive ability
can yield a sharpened branch stabbing weapon for killing small
mammal prey (Pruetzi and Bertolani, 2007), then how capable would
more encephalized early Homo have been at fashioning wooden
weapons and tools? A fourth question is directed to any who would
discount the very idea of large mammal hunting with wooden spears
by Pleistocene Homo: How can science ever determine when this
behavior actually began, if we allow our investigations to be guided
by ideology rather than evidence and if we do not ask such provocative
questions and then explore ways of answering them?

Moving beyond hunting, in creating a diurnal scavenging niche for
early Homo made possible by ER, Bramble and Lieberman (2004)
reason that ER would have aided early Homo in competitive
scavenging against hyenas, wild dogs (Lycaon pictus), and other
hominins. Yet, Lieberman et al. (2007: 441) seek to enhance their ER
scavenging niche by misrepresenting the timing of scavenging by
various carnivores, including spotted hyenas, as an exclusively
nighttime activity, or at least discounting their ability to run and
scavenge effectively during the day, stating that “With ER capabilities,
hominins may have had a previously unrecognized advantage
scavenging in open habitats during the day when other scavengers
are prevented from running long distances because of thermoregu-
latory constraints (hyenas confine their running to dawn, dusk and
night). Scavenged meat is always an ephemeral resource, requiring
speed.” Ironically, what started as endurance running now requires speed
running, and hunting/scavenging toward flying vultures by
cursorial carnivores is now prevented during the day, according to
this modified view—a view that comprehends the natural world not as
one of complexities, but as one of simple absolutes. In this case,
diurnal scavenging becomes a tortoise-and-hare race to the carcass,
with hominins and the various carnivores in equal numbers and
distribution on the landscape, but with only hominins able to persist
via diurnal running to the finish line.

Our own experiences in the field in Africa prompt a challenge to
detractors that the simple act of actually observing the behavior of
wild predators, prey and their ecological interactions (for even a
minimum of time) would erode such black-and-white certainty. Short
of that, even cursory survey of classic wildlife and paleoanthropologi-
cal literature highlights just how nuanced is carnivore behavior. True,
spotted hyenas are most active during the dusk to dawn hours,
particularly as predators, but they (and lions and wild dogs) often
locate and exploit scavenging opportunities during the daytime
by observing the activities of flying vultures and running to the indicated
locations (e.g., Schaller and Lowther, 1969; Kruuk, 1972; Schaller,
1972). Kruuk (1972: 108–113), for example, characterizes spotted
hyenas in the Serengeti as “better adapted to a scavenging existence
than any of the other large carnivores in the area,” noting “the hyenas’
inclination to scavenge by daylight” by “react(ing) to alighting
vultures more promptly than many other carnivores.” Thus, the
vision of an open niche for daytime scavenging by hominins using ER,
is hard to reconcile with reality in the natural world, or for
that matter, with the expanded carnivore guild of the Pleistocene.

At the same time, rather than branding our approach as side-
stepping relevant but inconvenient datasets, disagreeing parties
would better benefit paleoanthropological discourse on early
hominin carcass foraging by addressing the following substantive
points:

1. The falsification of the ER hunting hypotheses by boid–mortality
evidence;
2. The probable implications for Pleistocene Homo of a likely cause–
effect relationship between vegetational habitats and success rate of
human tracking;
3. The logic of assuming sophisticated tracking skills in early Homo
and their immediate ancestors, while discounting any intellectual
ability to ambush prey.

George Schaller (1972: 195) stated that “Predation is exceedingly
complex.” So is the reconstruction of ancient predation from fossil
teeth. Paleoanthropologists are well-advised to keep both declara-
tions of counsel in mind when constructing models of early hominin
carcass foraging.

Acknowledgments

HTB’s research was supported by the National Science Foundation
(USA), the L.S.B. Leakey Foundation, and the University of Wisconsin-
Madison. HTB thanks the Tanzania Commission for Science and
Technology (COSTECH) for permission to study the Olduvai collec-
tions from Mary Leakey’s research and to conduct research with
Hadzabe foragers, and the National Museums of Kenya for access to
Olduvai collections. TRP thanks his family for their support and
Francis Thackeray, Stephany Potze, and the Transvaal Museum for
permission to study the Gondolin and Kromdraai faunas. TRP’s
research was supported by the National Science Foundation (USA),
the LSB Leakey Foundation (USA), the Palaeontology Scientific Trust
(South Africa) and the University of Wisconsin-Madison (through a
Vilas Fellowship). We thank Manuel Domínguez-Rodrigo, José
Yazvedra, Gail Ashley, and Kathryn Remer for suggestions that
improved this paper. We also thank Teresa Steele for providing the
Modified Triangular Graph software used in the analysis. Special
thanks to Gary Haynes and an anonymous reviewer for their insightful
comments.

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