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Prey mortality profiles indicate that Early Pleistocene *Homo* at Olduvai was an ambush predator



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ABSTRACT

The prime-adult-dominated mortality profile of large bovids in the 1.8 Ma FLK Zinj assemblage, Olduvai Gorge, Tanzania, was recently attributed to ambush hunting by early *Homo* (Bunn, H.T., Pickering, T.R. 2010. *Quat. Res.* 74, 395–404). We now investigate a logical follow-up question: is enough known about the causes and pervasiveness of prime-adult-dominated mortality profiles (defined as >70% prime adults) from modern ecosystems and from archaeological sites to warrant their attribution solely to hominin hunting? Besides hominin hunting, three methods of scavenging could have provided the large bovids butchered at FLK Zinj: first-access scavenging from non-predator-related accidents; late-access passive scavenging from lion (or other) kills; early-access aggressive scavenging from lion (or other) kills.

We present new data on hunted prey from Hadza bow hunting (e.g., $N = 50$ impala; $N = 18$ greater kudu) near Lake Eyasi, Tanzania, and from San bow hunting ($N = 13$ gemsbok) in the Kalahari Desert, Botswana, documenting non-selective, living-structure profiles. We present new data on drowned wildebeest ($N = 175$) from Lake Masek, in the Serengeti, documenting many prime adults but also a significantly high percentage of old adults, unlike the profile at FLK Zinj. We also examine mortality profiles from modern African lions and from Old World Pleistocene archaeological sites, revealing that while prime-dominated profiles are present in some archaeological assemblages, particularly some Late Pleistocene European sites involving cervids, they are not documented from lion or other larger carnivore predation; moreover, living-structure profiles with prime adults representing ~50–60% of prey are common, particularly in African archaeological assemblages involving bovids hunted by humans. Although taphonomic bias, prey socioecology, and season of death may all influence mortality profiles, prime-dominated profiles require careful evaluation. The prime-dominated profile at FLK Zinj is significantly different from profiles formed by the three scavenging methods, which likely indicates hunting by Early Pleistocene *Homo*.

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1. Introduction

Patterns in the age at death, or mortality profiles, of prey animals at archaeological sites provide evidence of the evolution of human meat-foraging capabilities. Similarly, because modern carnivores exhibit size- and age-specific prey preferences, their known prey mortality profiles can be used to infer predator behavior in ancient, carnivore-generated bone assemblages. At relatively recent archaeological contexts from the last 100,000–50,000 years, the large animal hunting capability of humans armed with stone-tipped spears, atlatl darts, and bows and arrows, is not in question. The prey mortality profiles from such sites can help characterize mortality profiles resulting from human hunting with

projectile weaponry. However, at very ancient archaeological contexts, such as Early Pleistocene Oldowan sites, the meat-foraging capability of early *Homo* is contentious. This enduring “hunting and scavenging” debate can be resolved with the evidence of prey mortality profiles.

In an influential paper in which she developed the triangular graph method of displaying mortality data, [Stiner \(1990\)](#) stated that with rare exception, only human hunting, not carnivore predation or other natural processes, is known to produce a prime-adult-dominated mortality profile in which the proportion of prime adults exceeds ~70% of the prey sample. [Bunn and Pickering \(2010\)](#) reported a prime-dominated mortality profile for the heavily butchered, large bovids from the 1.84 Ma FLK Zinj site in Bed I of Olduvai Gorge, Tanzania. (In this paper, “large” and “size group 3” are used interchangeably to denote animals with live body weight between 250 and 750 pounds; e.g., [Bunn et al., 1988](#)). Because the FLK Zinj profile does not match what lions are known to kill,

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hypotheses of scavenging from lion kills are effectively falsified as a dominant factor at FLK Zinj, provided that modern Serengeti lion-kill data are representative of the prey preferences of lions in the present and of lions and other, extinct large felids in the past. The abundance of prime adults at FLK Zinj also effectively falsifies the hypothesis of hunting by endurance running as proposed by Bramble and Lieberman (2004), and of scavenging from natural, non-predator-related dead animals, provided that we understand fully the mortality profiles most likely to result from such alternative sources. Bunn and Pickering (2010) concluded that Early Pleistocene *Homo* probably obtained the large bovids at FLK Zinj by effective ambush hunting, possibly with wooden spears, but we want to acknowledge here the clear need for a wider range of mortality data to test their conclusion.

Is that provocative conclusion the only plausible explanation for the FLK Zinj pattern? To better understand the prime-dominated concept and to search for alternative explanations for the prime-dominated pattern at FLK Zinj, we present new empirical mortality data from our research with modern African hunter–gatherers and with mass drowning of large ungulates (wildebeest). We then examine available mortality data on the prey preferences of modern lions. Finally, we summarize prey mortality data from several classic Late Pleistocene archaeological sites, including Middle Stone Age Klasies River Mouth, S. Africa, Upper Paleolithic (Aurignacian) El Castillo, Spain, and Upper Paleolithic (Aurignacian) Abri Pataud, France. We chose these sites because detailed mortality data are available from them, which facilitates comparative analysis, and because stone spear points are present, which probably indicates the use of stone-tipped spears as hunting weapons. Comparative analysis of these varied case studies and the prime-dominated mortality profile of large bovids at FLK Zinj reveals that (1) the FLK Zinj pattern does not match mortality profiles from lion predation or mass drownings, which effectively falsifies hypotheses of those methods of scavenging, and (2) the FLK Zinj pattern does strongly match mortality profiles from ethnographic and Late Pleistocene archaeological case studies of human hunting with projectile weapons.

Interestingly, these case studies of human hunting reveal living-structure rather than extremely prime-dominated mortality profiles. Past and present human hunting can certainly produce prime-dominated profiles, as reasonably argued by Stiner (1990), but we conclude that living structure profiles are a more common result of human hunting with projectile weapons. The living structure profile of red deer at Upper Paleolithic El Castillo led archaeologists there to characterize hunting capability as the “effective” killing of prime adults (Pike-Tay et al., 1999). The label “effective” is being used to mean hunting capability sufficient to kill any age of prey animal, including many robust, prime adults. We characterize our ethnographic case studies the same way, and conclude that the mortality profile for the large bovids at FLK Zinj likely reflects the same hunting strategy: ambush hunting.

2. Background

Mortality profile analysis has a long history in archaeological and paleontological research (e.g., Voorhies, 1969; Lyman, 1994), and it is particularly well developed in North America and Europe, though less so in Africa. Klein’s long-term research with many Pleistocene bone assemblages in southern Africa provides a major exception (e.g., Klein, 1976; Klein et al., 2007). Klein’s approach for documenting mortality profiles relies on the measurement of tooth crown heights and their display as age-frequency histograms in which the data on age at death are grouped into 10 percent increments of the animal’s potential life span. The archaeological histograms are compared to two idealized age/mortality profiles

known from biology: (1) catastrophic profiles reflecting the living structure of a population, or in an ancient context, a catastrophically killed population in which individual age or health conferred no survival advantage; (2) attritional profiles derived from the living structure of a population reflecting the commonest mortality over time of the weakest or most vulnerable very young or very old individuals, rather than robust prime adults. When ancient mortality profiles deviate from the two idealized schematic profiles, as they often do, analysis and interpretation can prove challenging.

The introduction of triangular graphing into mortality profile analysis by Stiner (1990) provided significant advantages over age-frequency histograms. This approach involves grouping the mortality data into three broad segments of an animal’s life span: juvenile, prime adult, and old adult. One sample point on the triangular graph expresses the percentage of juveniles, prime adults, and old adults established through study of the teeth in an assemblage. This facilitates comparative analyses, because many sample points can be displayed on the same graph. Using published mortality data on the prey preferences of modern carnivores, Stiner was able to show that carnivore prey data plotted in two adjacent but separate zones of the triangular graph and that this could be largely attributed to hunting method. Cursorial predators plotted on the lower left zone of the triangle as attritional (or u-shaped) profiles, reflecting their known selectivity for the more vulnerable juveniles and old adults; ambush predators mostly plotted on the lower right zone of the triangle as catastrophic (or living structure) profiles, reflecting non-age-selective predation from a prey population. Stiner also interpreted prey profiles from Italian Middle and Upper Paleolithic archaeological sites as evidence of scavenging and hunting, including selective, prime-dominated hunting.

Steele and Weaver (2002) recognized that the plotting of sample points on a triangular graph did not take variable sample sizes into account, making the proximity of plotted points difficult to evaluate, and they developed the modified triangular graph software to do so. Instead of plotting a sample point, the software uses bootstrapping and draws a density contour around the sample points that approximates a 95% confidence interval and is sensitive to sample size. Small samples yield large density contours and vice versa. Non-overlapping density contours indicate with 95% probability that the samples being compared did not come from the same source. Weaver et al. (2011) provide further refinement to the modified triangular graph approach.

Bunn and Pickering (2010) used modified triangular graphing to analyze fossil ungulate mortality data from the FLK Zinj assemblage and other Oldowan archaeological sites in Bed I, Olduvai Gorge, Tanzania. The logic of the analysis was straightforward: if, as advocates of scavenging hypotheses contend, hominins did not hunt but merely scavenged from tree-stored leopard kills for smaller bovids and from lion kills for larger bovids, then the mortality profiles for the heavily butchered smaller and larger bovids at FLK Zinj should match what modern leopards and lions are known to kill. The mortality profiles do not match, and the statistically significant differences led Bunn and Pickering (2010) to conclude that Early Pleistocene *Homo* was a successful ambush hunter, possibly using wooden spears.

In this paper, we focus on the apparent prime-dominated mortality profile for large bovids at FLK Zinj, which we seek to evaluate further through comparisons with other actualistic and archaeological data. For decades, the larger bovids from FLK Zinj have been the principal evidence used in the hunting and scavenging debate. We argue that the main reason the debate has endured is that the two conventional classes of taphonomic data employed – skeletal element profiles and bone surface modifications – are insufficient to differentiate convincingly among different methods of acquiring carcasses in the first place. We

identify four broad methods of carcass acquisition that Early Pleistocene *Homo* could have practiced: (1) first-access scavenging from animals dead from causes other than predation; (2) passive scavenging from defleshed and abandoned felid kills; (3) aggressive, confrontational or power scavenging from intact or nearly intact felid kills; (4) hunting by, for example, ambush or endurance running methods. Additional, specific methods could, of course, be defined along this continuum. The point is that three of the four broad methods (numbers 1, 3, 4) would yield essentially intact dead animals; realistically, would these have been handled differently by hominins, and if not, how can skeletal profiles and bone surface modifications distinguish effectively among them? Only one method, passive scavenging from felid kills, would yield defleshed and often partial carcass residues and likely different skeletal and modification patterns. We do contend that the large bovid evidence from FLK Zinj – the abundance of the very uppermost limb elements that felids deflesh rapidly and the abundance of defleshing cut marks on them – effectively falsifies passive scavenging as a significant explanation of the meat-foraging capabilities of early *Homo* at Olduvai. That argument was made long ago (e.g., Bunn and Kroll, 1986, 1988; Bunn and Ezzo, 1993). More recently, the only other alleged foundation of the passive scavenging hypothesis – an apparent high incidence of carnivore gnawing on the limb elements from FLK Zinj – was called into question when Domínguez-Rodrigo and Barba (2006) demonstrated that most of what Blumenschine (1995), Blumenschine et al. (2007), and Capaldo (1997) had called carnivore gnaw marks were actually misidentified products of biochemical etching. To resolve such lingering issues, remaining advocates of passive scavenging (e.g., Blumenschine et al., 2012; Pante et al., 2012) could try to address more thoroughly the alternative, current reconstructions and evidence of more advanced meat-foraging capabilities of early *Homo*. Another productive approach is for more independent researchers to investigate the

defining characteristics of carnivore gnaw marks and their mimics on fossil bones, and to then apply those findings in new analyses of Early Pleistocene archaeological bone assemblages (e.g., Parkinson, 2013).

This is where mortality profile analysis has the exciting potential to achieve a breakthrough and bring the longstanding hunting and scavenging debate to closure. Prey mortality profiles can distinguish among the four broad methods of carcass acquisition outlined above, because the methods are linked to a range of testable mortality predictions, as follows. (1) First-access scavenging from animals that died from causes other than predation, such as accidents in which relative strength or health might confer survival advantage to some individuals, should yield some individuals of all ages with an abundance beyond natural population proportions of the weakest or most vulnerable young juveniles and old adults. (2) Passive scavenging from abandoned felid kills and (3) aggressive scavenging from felid kills should match what felids are known to kill. In the case of leopards preying on smaller bovids, Schaller's (1972) data indicate a non-selective, living structure mortality profile. Serengeti lions preying on large, size group 3 wildebeest in Schaller's (1972) study kill a significantly higher proportion of old adults (33%) than occurs in the Serengeti wildebeest prey population (8%; Table 1). Thus, the mortality profiles of large bovids scavenged from lions should plot near the upper (old age) end of the living-structure zone on a triangular graph because of an elevated number of old adult prey. Mortality profiles from (4) hunting by early *Homo* are more challenging to predict. Persistence hunting by endurance running, for example, should, like other forms of cursorial predation, yield abundance of the weakest, most vulnerable young juveniles and old adults. Ambush hunting, if selective and efficient, should yield an abundance of the nutritionally most attractive prime adults; non-selective ambush hunting should yield a living-structure mortality profile.

Table 1
Modern and archaeological prey mortality data used in Figs. 3–6.

| | Young juveniles | Subadults | Early prime | Late prime | All juveniles | All prime adults | Old adults | N or MNI |
|---|-----------------|-----------|-------------|------------|---------------|------------------|------------|----------|
| FLK Zinj, Olduvai Gorge, Tanzania | | | | | | | | |
| Bovids (size 3) | 2 | 3 | | | 5 | 12 | 2 | 19 |
| Klasies River Mouth, South Africa | | | | | | | | |
| Bovids (size 3) | | | | | | | | |
| Roan | 29 | 10 | | | 39 | 28 | 11 | 78 |
| Hartebeest | 3 | 2 | | | 5 | 3 | 0 | 8 |
| Topi | 0 | 3 | | | 3 | 2 | 0 | 5 |
| Wildebeest | 8 | 4 | | | 12 | 7 | 1 | 20 |
| Greater Kudu | 8 | 2 | | | 10 | 3 | 0 | 13 |
| Bovid (size 3) total | | | | | | | | |
| w/infants | 48 | 21 | | | 69 | 43 | 12 | 124 |
| w/o infants | | 21 | | | 21 | 43 | 12 | 76 |
| Abri Pataud, France | | | | | | | | |
| Aurignacian | | | | | | | | |
| Reindeer | 11 | 15 | | | 26 | 60 | 7 | 93 |
| El Castillo, Spain | | | | | | | | |
| Aurignacian | | | | | | | | |
| Red Deer | | | | | | | | |
| Level 18c | 1 | 9 | | | 10 | 18 | 1 | 29 |
| Level 18b1 | | 2 | | | 2 | 5 | 1 | 8 |
| Level 18b2 | | 3 | | | 3 | 11 | 2 | 16 |
| Aurignacian Total | | | | | | | | |
| Red Deer | 1 | 14 | | | 15 | 34 | 4 | 53 |
| Hadza-killed bovids 2008–09, Tanzania | | | | | | | | |
| Impala | 6 | 9 | 24 | 7 | 15 | 31 | 4 | 50 |
| Greater Kudu | 3 | 3 | 7 | 3 | 6 | 10 | 2 | 18 |
| Kua-killed bovids (size 3), Kalahari, Botswana | | | | | | | | |
| Gemsbok | 3 | 2 | 3 | 4 | 5 | 7 | 1 | 13 |
| Kafue Lion-killed bovids (size 3), Zambia | | | | | | | | |
| Bovid (size 3) | | | | | | | | |
| Hartebeest | 15 | 2 | | | 17 | 26 | 8 | 51 |
| Kudu | 2 | | | | 2 | | | 2 |

Table 1 (continued)

| | Young juveniles | Subadults | Early prime | Late prime | All juveniles | All prime adults | Old adults | N or MNI |
|-----------------------------|-----------------|-----------|-------------|------------|---------------|------------------|------------|----------|
| Wildebeest | 5 | 1 | | | 6 | 8 | 3 | 17 |
| Waterbuck | 4 | | | | 4 | 6 | 3 | 13 |
| Roan | 4 | | | | 4 | 6 | 7 | 17 |
| Sable | 5 | 1 | | | 6 | 8 | 2 | 16 |
| Bovid (size 3) total | | | | | | | | |
| w/infants | 35 | 4 | | | 39 | 54 | 23 | 116 |
| w/o infants | | 4 | | | 4 | 54 | 23 | 81 |
| Serengeti, Tanzania | | | | | | | | |
| Wildebeest | | | | | | | | |
| Lion-killed | | 50 | | | 50 | 78 | 62 | 190 |
| Drowned Masek | | 8 | | | 8 | 100 | 67 | 175 |
| Serengeti herd | 32 | 50 | | | 82 | 104 | 17 | 203 |

3. Materials and methods

The mortality data that we have compiled for comparative analysis with the FLK Zinj larger bovid assemblage includes actualistic data from our own current and past field research in eastern and southern Africa, published data from the modern wildlife literature, and published data from Late Pleistocene archaeological sites in South Africa, Spain, and France, as follows.

3.1. Lake Masek and mass drownings of wildebeest

Located in the southern Serengeti Plains at the headwaters of Olduvai Gorge, Lake Masek lies across the annual migration route of the wildebeest. The determined wildebeest follow the migration route whether Lake Masek is full of water or not, and this leads to accidental mass drownings. One documented scenario involves the behavior of mothers in herds of mostly adult female wildebeest and their young. A mother jumps into the lake and swims across, and baby dutifully follows. Being larger and stronger, the mother reaches the other bank first and looks unsuccessfully for baby. She jumps in and swims back across the lake to the starting point. If that baby manages to reach the other bank, it does not find its mother and jumps back in to look for her. Eventually, this leads to a lot of dead, bloated wildebeest out in the lake, and the prevailing wind blows them to the north shore, where there are skeletal remains of literally hundreds of wildebeest from multiple drowning episodes over the years. Indeed, mass drownings modeled after Lake Masek have been suggested as a plausible source of the large bovinds at FLK



Fig. 1. Skeletal remains of drowned wildebeest along the shoreline of Lake Masek, in the southern Serengeti plains of Tanzania.

Zinj based on skeletal profiles (Capaldo and Peters, 1995). To test that idea, we traveled to Lake Masek in July, 2012, to document the mortality profile of the drowned wildebeest. We sampled approximately one kilometer of lakeshore and aged 175 wildebeest skulls (Fig. 1).

3.2. Hadza foragers and their prey at Lake Eyasi, northern Tanzania

The foraging adaptations of the Hadza are well known to anthropologists. Living in a savanna-bush-woodland setting and armed with powerful long bows and metal-tipped, poisoned arrows (Fig. 2), the Hadza hunt a wide range of large mammals and consume prodigious amounts of meat. Since 1984, Bunn has conducted research on diverse topics with the Hadza, including ethnoarchaeology, behavioral ecology, and archaeology (e.g., Bunn et al., 1988; Bunn, 1993, 2001, 2007; Murray et al., 2001; Schoeninger et al., 2001). Research in 1986 and 1988 yielded a hunted and scavenged sample of 110 prey animals. To achieve a uniquely large dental sample of Hadza prey, annual research for the past five years has included revisiting recently abandoned Hadza base camps with the informants who resided at them and collecting teeth from several hundred prey animals. We report here on the 2008–09 sample of impala (*Aepyceros melampus*; $N = 50$) and greater kudu (*Tragelaphus strepsiceros*; $N = 18$).

3.3. Kua San foragers and their prey in the east-central Kalahari Desert, Botswana

In 1985–87, Bunn and Kroll directed an ethnoarchaeological research project focused on camp structure and bone food refuse in



Fig. 2. Metal-tipped and poisoned arrows of Hadza foragers at Lake Eyasi in northern Tanzania.

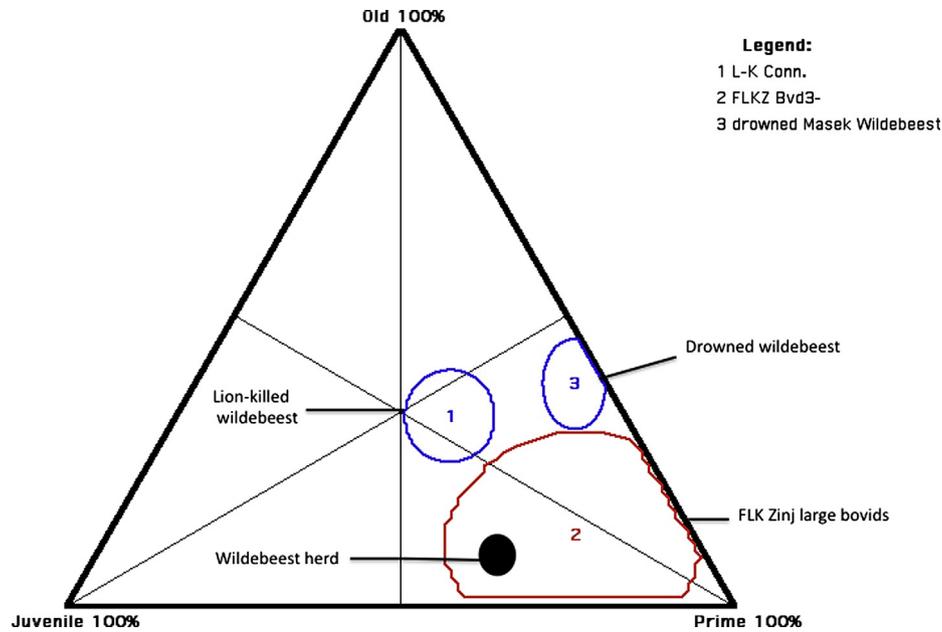


Fig. 3. Triangular graph comparing the mortality profile of large bovids from the 1.84 Ma FLK Zinj archaeological site at Olduvai Gorge, with several modern mortality profiles including Serengeti lion-killed wildebeest ($N = 190$; data from Schaller, 1972), the living structure of the Serengeti wildebeest herd (data from Sinclair, 1977), and new empirical data from the drowned wildebeest at Lake Masek ($N = 175$).

the East-Central Kalahari, where the Kua subsisted in an under-productive and harsh environment (e.g., Bartram et al., 1988). Hunters employed persistence hunting and snaring, and they used small bows and powerful arrow poison to kill large prey. We report here on the 1986 rainy season sample of hunted gemsbok (*Oryx gazella*; $N = 13$).

3.4. Prey mortality data from literature sources

The literature on wildlife research provides detailed prey mortality data less commonly than is found in the archaeological literature. The classic study of the Serengeti lion population (Schaller, 1972; Sinclair, 1977) includes a wealth of high-resolution mortality data, which Bunn and Pickering (2010) used. To expand the ecological coverage, we sought additional, large samples of mortality data on lion prey. Many long-term studies fail to report age structures in the juvenile-prime-old format, and so had to be rejected. Fortunately, Mitchell et al. (1965) conducted an impressive study at the Kafue National Park, Zambia, that reports on 650 prey animals of lions (and other predators) and does present mortality data in adequate detail for analysis here.

Many archaeological studies include detailed prey mortality data. We include three Late Pleistocene sites from Africa and Europe to illustrate a more widespread mortality pattern resulting from human hunting, in these cases probably with stone-tipped spears. Klasies River Mouth is a series of caves and rock shelters excavated in the 1960s by Singer and Wymer (1982). A composite section of 18 m of deposit formed during the 60–70,000 year span of the last interglacial, starting ~130,000 years before the present. During that period, anatomically modern *Homo sapiens* left a rich record of Middle Stone Age (MSA) artifacts and faunal remains at the site. Klein (e.g., 1976) has published extensively on the large assemblage of faunal remains, and his methodology deserves comment. He combined the mortality data by species for the entire 18 m-thick deposit spanning 60–70,000 years, rather than investigating stratigraphic sub-sets representing fewer behavioral events. In some cases, he referred to minimum numbers of

individuals, whereas in other instances, he used “ N ” for his sample size. It is clear that in the latter instances, he used the total numbers (lefts and rights) of a particular tooth (e.g., lower third molar) of a species and not the minimum number of individuals. This results in a potential overrepresentation of age-classes with well-preserved individuals. Klein’s publications have emphasized mortality profiles of very large eland (*Taurotragus oryx*) and Cape buffalo (*Syncerus caffer*). Our focus here is on the size group 3 bovids that are comparable in size to nearly all other animals in our study, for which we used the data from Klein (1976).

El Castillo and Abri Pataud are extensively studied cave sites in northern Spain and southwestern France, respectively. We report on Upper Paleolithic (Aurignacian) mortality data on red deer (*Cervus elaphus*) from El Castillo (Pike-Tay et al., 1999) and on reindeer (*Rangifer tarandus*) from Abri Pataud (Spiess, 1979).

4. Results

Table 1 presents the prey mortality data used in our analysis. For comparative purposes, the triangular graphs (Figs. 3–6) include the non-overlapping mortality profiles of Serengeti lions and of FLK Zinj large bovids from Bunn and Pickering (2010).

Fig. 3 plots the mortality profiles of the drowned wildebeest at Lake Masek and of the living Serengeti wildebeest herd. There are abundant prime adults in the drowned sample, but like the Serengeti lion prey, the drowned sample includes a significantly elevated frequency of old adults. The very low frequency of juveniles in the drowned sample is likely due to taphonomic loss, as these bones are easily consumed by large predators. Alternatively, the drowned sample that we documented, which includes many male animals, may result from episodes mainly involving bachelor herds. To avoid any taphonomic bias, Table 2 reduces the analysis to a comparison of prime adults to old adults. The Fisher’s Exact test reveals that the drowned sample is not significantly different from the lion prey, but both the drowned sample and lion prey are significantly different from the live herd and from FLK Zinj.

Table 2

Fisher's Exact test comparing prime and old adults in lion prey and in FLK Zinj with other mortality profiles.

| | Prime | Old | Ratio | P |
|---|-------|-----|--------|--------|
| Serengeti lions mortality profile compared with other mortality profiles | | | | |
| Lion | 78 | 62 | 1.3: 1 | |
| FLK Zinj | 12 | 2 | 6: 1 | 0.0439 |
| Hadza-killed impala | 31 | 4 | 7.8:1 | 0.0003 |
| Herd wildebeest | 104 | 17 | 6: 1 | 0.0001 |
| Lake Masek wildebeest | 100 | 67 | 1.5: 1 | 0.487 |
| FLK Zinj mortality profile compared with other mortality profiles | | | | |
| FLK Zinj | 12 | 2 | 6:01 | |
| Hadza-killed impala | 31 | 4 | 7.8:1 | 1 |
| Herd wildebeest | 104 | 17 | 6:01 | 1 |
| Klasies size group 3 bovids | 43 | 12 | 3.6:1 | 0.718 |
| UP Abri Pataud reindeer | 60 | 7 | 8.6:1 | 0.65 |
| UP El Castillo red deer | 34 | 4 | 8.5:1 | 0.654 |
| Lake Masek wildebeest | 100 | 67 | 1.5: 1 | 0.0834 |

Fig. 4 plots the mortality profile of lion prey from the woodlands and edaphic grasslands of the Kafue ecosystem. The pooled sample of different large bovid taxa has a strong similarity to the Serengeti lion-killed wildebeest in that both exhibit an elevated frequency of old adults compared to their frequency in a living herd.

Fig. 5 presents the mortality profiles from Hadza and Kua bow hunting. Interestingly, both ambush and encounter hunting by these foragers using sophisticated, very lethal weaponry produce a living-structure mortality profile. Their strategy is one of opportunistic hunting rather than passing up shots at less attractive juveniles or old adults with the expectation and intention of waiting to shoot a prime adult. They do not pass up shots, and this provides a non-selective, living-structure mortality profile. These known cases of hunting by modern foragers overlap with the FLK Zinj profile and are statistically indistinguishable, but like FLK Zinj, the forager hunting profile is significantly different from the profile for lion prey (Table 2).

Fig. 6 presents the mortality profiles from the three Late Pleistocene archaeological sites where MSA or Upper Paleolithic hunters wielding stone-tipped spears were probably responsible for the prey profiles. Once again, the pooled, large bovid sample from Klasies, the red deer sample from El Castillo, and the reindeer sample from Abri Pataud, all exhibit living-structure mortality profiles that do not differ significantly from the profiles from the ethnographic bow hunters and FLK Zinj (Table 2).

5. Discussion and conclusions

From comparative analysis of these varied mortality profiles, we see the emergence of a strong pattern and a straightforward explanation for FLK Zinj and the meat-foraging capabilities of Early Pleistocene *Homo*: effective ambush hunting. We have documented what the mortality profiles from modern bow hunting look like from an ecological setting closely analogous to that reconstructed for Early Pleistocene Olduvai (Lake Eyasi; Ashley et al., 2010a, b; Barboni et al., 2010) and from a contrastive ecological setting of drier and open grassland (Kalahari). In both cases, the prey mortality profiles are the same, and FLK Zinj resembles them quite well statistically. We have documented the mortality profiles from probable spear hunting at several Late Pleistocene archaeological sites. They, too, are living-structure profiles, and FLK Zinj resembles them as well.

Notably, FLK Zinj is a statistically significant mismatch to other likely sources for the large bovids, including first-access scavenging from mass drownings, scavenging from lion kills, and persistence hunting. Bunn and Pickering (2010) labeled the FLK Zinj pattern “prime-dominated”, and technically it is; the fairly small sample includes ~72% prime adults which is higher than the 70% boundary between living structure and prime-dominated zones on a triangular graph. While the large density contour fills the prime corner of the graph, this is largely a product of sample size. That said, seven

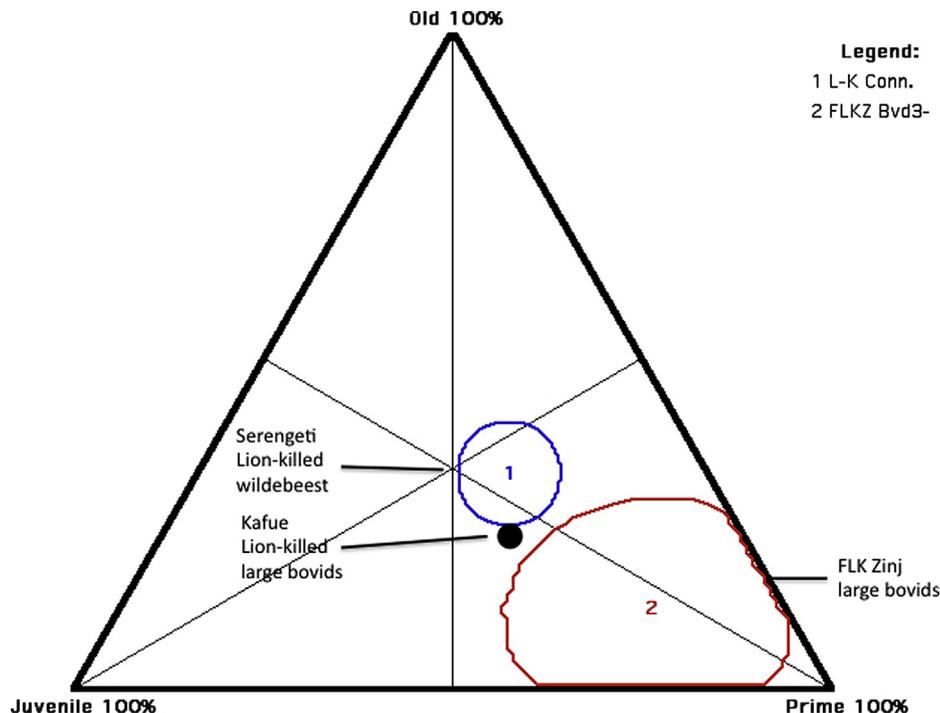


Fig. 4. Triangular graph comparing the mortality profiles of large bovids from the 1.84 Ma FLK Zinj archaeological site at Olduvai Gorge, Serengeti lion-killed wildebeest, and lion-killed large bovids from Kafue National Park, Zambia ($N = 410$ lion kills; data from Mitchell et al., 1965). Unlike FLK Zinj, which resembles a living herd structure, both lion-killed mortality profiles are elevated in old adults.

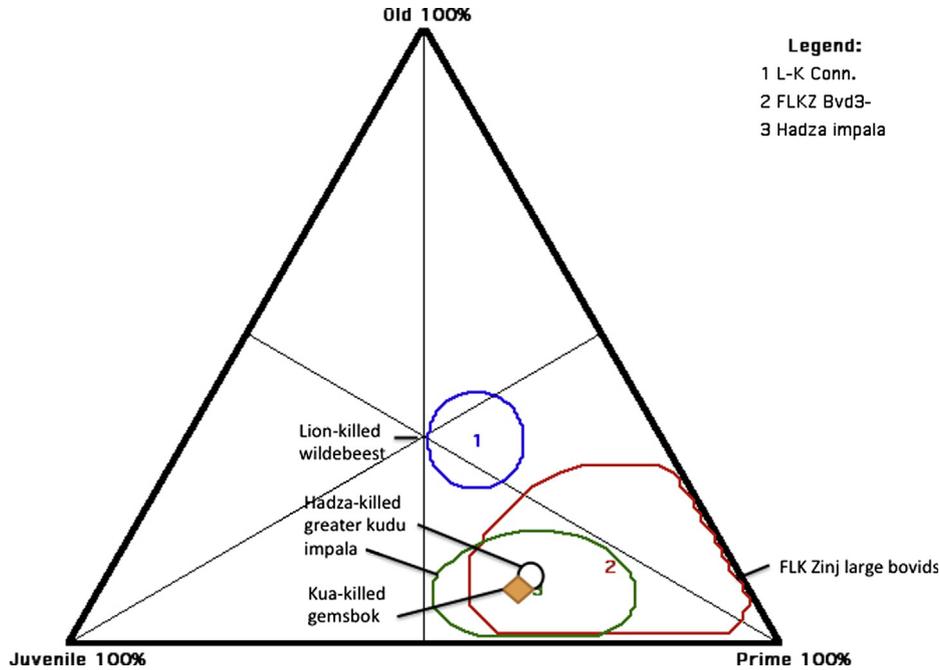


Fig. 5. Triangular graph comparing the mortality profiles of large bovids from the 1.84 Ma FLK Zinj archaeological site at Olduvai Gorge and Serengeti lion-killed wildebeest with new empirical data on the mortality profiles resulting from bow hunting by modern Hadza and Kua foragers from Lake Eyasi, Tanzania, and the east-central Kalahari Desert, Botswana, respectively. For the Hadza, prey samples are $N = 50$ for impala and $N = 18$ for greater kudu; for the Kua, prey sample is $N = 13$ for gemsbok.

of seven adult waterbuck at FLK Zinj are prime adults. Still, there is considerable overlap with the living-structure zone of the graph and no statistical separation from the hunted, living-structure cases discussed above. Using the label “prime-dominated” does risk over-emphasizing the idea of selectivity in choosing prime adults and not other ages of prey. What is frequently labeled “prime-

dominated” and might imply crossing a 70% prime “Rubicon” to be positioned in the 70–100% prime range, actually refers to a less extreme pattern at the high end of the living-structure zone of the graph. Europeanists refer to prime-adult proportions in the ~low-to mid-60s% range as “prime-dominated” and attribute the pattern to effective, non-selective ambush hunting of prime-adult prey

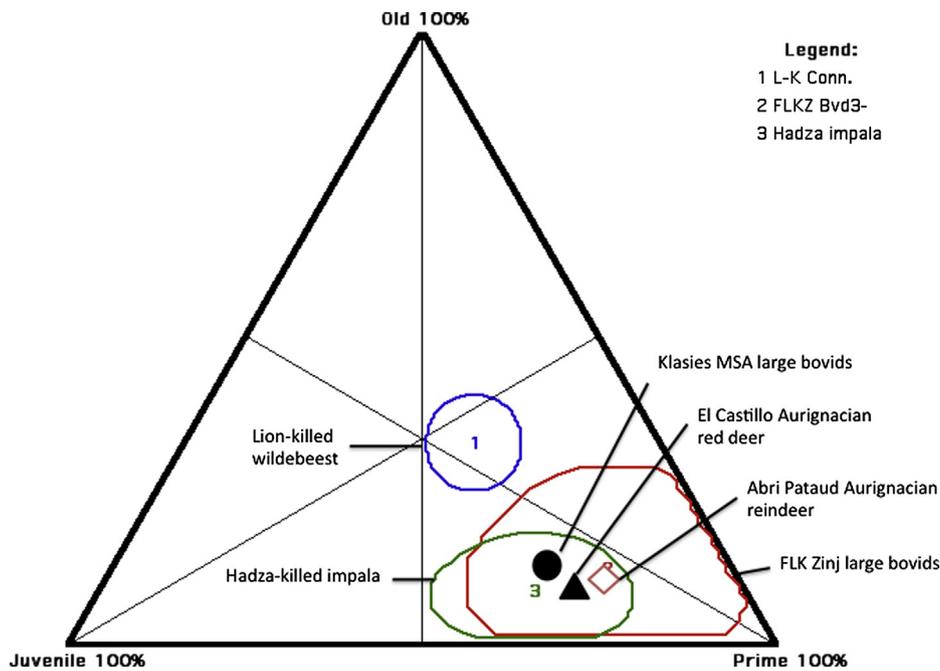


Fig. 6. Triangular graph comparing the mortality profiles of large bovids from the 1.84 Ma FLK Zinj archaeological site at Olduvai Gorge, Serengeti lion-killed wildebeest, and Hadza-killed impala, with published mortality data from three Late Pleistocene archaeological sites where humans likely hunted with stone-tipped spears. For Middle Stone Age Klasies River Mouth in South Africa, data are from Klein (1976). For Aurignacian El Castillo in Spain, data on red deer prey are from Pike-Tay et al. (1999). For Aurignacian Abri Pataud in southwest France, data on reindeer prey are from Spiess (1979). All three of the Late Pleistocene archaeological profiles plot in the living-structure zone, showing strong similarities to both FLK Zinj and Hadza-killed impala.

(e.g., Pike-Tay et al., 1999). We argue that the same mortality pattern in anthropogenically-derived large prey at Early Pleistocene FLK Zinj reflects a similar capability for effective ambush hunting by early *Homo*.

Yet another alternative explanation for the mortality profile at FLK Zinj merits consideration: differential transport of prime adult large bovids. Different individuals (and their constituent body parts) in an ungulate species vary in their nutritional quality as potential human food according to age, sex, and season. Decisions regarding what prey to transport home and what to abandon elsewhere by hunters aware of these differences can lead to selective utilization of the nutritionally best quality prey, which are often prime adults. Both ethnographic (e.g., Binford, 1978) and archaeological (e.g., Speth, 1983; Speth and Tchernov, 2001) case studies document this dynamic process. In the Hadza setting, for example, large, size 3 ungulate carcasses are commonly field-butchered and transported entirely back to base camps, where even unwieldy axial bones such as vertebrae and ribs are chopped into pieces and boiled for their fat (Bunn et al., 1988; Bunn, 1993; Bunn, 2007). For the Hadza, the “food item” is the entire carcass, not its constituent parts, and social group size is sufficiently large that size 3 carcasses are commonly transported entirely and without much concern over transport costs. Yet, within their size group 3 prey, different taxa are handled differently, and it has little to do with the energetic costs of transport. Zebra, a common and favorite food, are almost always transported entirely, or nearly so, but transport of the similarly-sized wildebeest, an uncommon species regarded as having poor-quality marrow, favors only meat and postcranial axial parts. Factors influencing decision-making about utilization and transport are complex, and many nuances observable ethnographically are unknowable archaeologically. Is it, therefore, plausible that prey transport decisions by Early Pleistocene *Homo* concerning prey quality led to selective transport favoring prime adult prey, whether hunted or scavenged, from points of acquisition to FLK Zinj?

To address that question, we envision two stages in the acquisition and processing of prey in which a disproportionate abundance of prime adults might result from hunters' decisions. First, at the hunting stage, under circumstances in which a group of prey were already disadvantaged by being mired in some natural trap (or intentionally driven into a trap by hunters) and unable to flee, the hunters might recognize that they had the luxury to pick-and-choose the best-quality animals from a larger group than they could utilize. Second, at the field butchery and transport stage, it is conceivable that hunters in possession of multiple prey carcasses would recognize a quality differential according to age and sex, and then selectively transport home only the best-quality prime adults. In both of these hypothetical circumstances, the key factor stimulating a disproportionate abundance of prime adults is the access to multiple prey animals of different nutritional quality at one time. The practice by Nunamiut Eskimos of selecting for transport desired animal parts from frozen meat caches of multiple carcasses illustrates this (Binford, 1978), as does Speth's (1983) archaeological reconstruction of bison utilization at the Garnsey site. However, as we have reported from our case studies of tropical foragers, ambush hunting typically yields one animal at a time and produces a living-structure mortality profile.

Hunters with the weaponry to kill prey of any age routinely kill many prime adults (~60–70% in Tables 1 and 2) because there are many of those in a prey population, not because they are selecting them and passing up others. Lions also routinely kill many prime adults (~45%), but notably, they also kill a disproportionately large number of old adults (~28%) compared to a natural population (<10%; Tables 1 and 2). Selective scavenging of prime adults might also yield a disproportionate abundance of prime adults in a

hypothetical scenario in which hominins, having survived driving lions from their kill, then inspect their prize, find it wanting, reject it, and generously invite the lions back to finish their meal.

We consider it unlikely that in either a hunting or scavenging scenario yielding one animal at a time, foragers already possessing a sought-after carcass, even if it is not the best quality, are going to reject it and leave empty-handed. What if instead, some selective transport favoring prime adults occurs, involving more complete transport of primes but only partial transport of juveniles and old adults? Then, we would expect skeletal element profiles to reflect that. If, for example, hominins favored high-yield limb elements for transport over low-yield hemimandibles of non-primes, then limbs should occur in higher proportions than hemimandibles. Precisely the opposite pattern, of more individuals represented by hemimandibles than by limb elements, has been documented at the FLK Zinj site (Bunn and Kroll, 1986, 1988). Thus, the FLK Zinj hemimandibles probably provide a representative measure of the prey animals that hominins obtained. Judging from the very similar mortality profiles documented in widespread Late Pleistocene and more recent hunting case studies in which human hunting is not in doubt, we suggest that this ambush hunting dynamic and the living-structure mortality profiles it produces were widespread in the past.

We contend that this evidence points to one clear explanation: Early Pleistocene *Homo* was an effective ambush hunter whose meat-foraging capability has been significantly underestimated by some paleoanthropologists (and others). We suggest a possible reason why: early *Homo* has an image problem! Who was early *Homo*, how many species were present, and what was their temporal and geographic range? Paleoanthropologists struggle to reach consensus on this topic (e.g., Wood and Collard, 1999; Wood, 2009; Lordkipanidze et al., 2013). Who produced Oldowan tools, and who was responsible for the butchered large bovids at FLK Zinj? One popular image of early *Homo* is OH 62 and the beautiful oil painting of her by Matternes that graces the cover of *Lucy's Child: The Discovery of a Human Ancestor* (Johanson and Shreeve, 1989). She is shown clutching an Oldowan tool and towering over the surrounding vegetation and landscape. OH 62, a very fragmentary “partial skeleton” (Johanson et al., 1987) from Bed I at Olduvai and often included in *Homo habilis*, is still the most complete individual of early *Homo* known prior to WT-15000 (aka the Turkana Boy or early *Homo erectus*), but that does not mean that her species made most Oldowan tools or butchered anything at FLK Zinj. If we knew that her species was the predominant or sole Oldowan toolmaker, then we could understand any reluctance to accept a reconstruction of ambush hunting of large bovids with wooden spears. The problem is that she only stood one meter tall and probably lacked both the critical mass and strength necessary to harm large, wildebeest-sized bovids.

Achieving hunting success with large bovids likely necessitated a larger and stronger species of early *Homo* than the one OH 62 represents because it required that two conditions be satisfied: (1) getting close enough to inflict a mortal wound, and (2) having the technology to do so. Ambush hunting from bushes on the ground or, perhaps better, from the low branches of trees along active game trails, would alleviate the distance issue. Large ungulates expect attack from terrestrial predators, and their vigilance is consequently directed horizontally, not upward where a motionless hominin hunter would be difficult to detect even at short distances of five to ten meters or less. We suggest that wood-tipped spears would have provided the lethal weapon for short-distance throwing. No wooden spears of Early Pleistocene age have been discovered and preservational biases make this unlikely, but there are some intriguing clues of an Early Pleistocene wood technology, including microwear evidence of sawing or

scraping wood from ~1.5 Ma at Koobi Fora (Keeley and Toth, 1981), and wood phytolith evidence on stone tools of about the same age from Peninj (Domínguez-Rodrigo et al., 2001). Experimental work with wooden spears indicates that impacts can produce distinctive bone damage (Smith, 2003), and more experimental research is warranted.

In addition to *H. habilis*, there are larger, alternative species of early *Homo* known from Bed I at Olduvai and from the East African Rift Valley several hundred miles to the north during the time span when Bed I formed. At Olduvai, OH 65, which has been compared to *Homo rudolfensis* from the Turkana Basin (Blumenschine et al., 2003), establishes that a large-bodied species of *Homo* and a more likely producer of the Oldowan and FLK Zinj, was present when Bed I formed. Moreover, remains of early *H. erectus* have been identified from the Turkana Basin by ~1.9 Ma (Wood and Collard, 1999). Although *H. erectus* fossils have not been found in the rather sparse hominin fossil sample known from Bed I, we think it is likely that its early distribution was more widespread than the Turkana Basin, and that it likely existed elsewhere along the Rift Valley. Thus, our working hypothesis is that *H. erectus* could also have been present in the Olduvai Basin as a plausible Oldowan toolmaker and hunter. Perhaps they only foraged seasonally at Olduvai, where they were attracted to the oasis-like freshwater spring area near FLK (Ashley et al., 2010b), left an Oldowan archaeological record, and departed. If either of these hominins standing around ~1.6–1.8 m tall were responsible for FLK Zinj, that changes the game significantly. Adjust the image of who produced the FLK Zinj site to include a robust, large-bodied *Homo*, and our reconstruction of ambush hunting and killing large bovids with wooden spears may not be so provocative after all.

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