



Methodological recommendations for ungulate mortality analyses in paleoanthropology

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ABSTRACT

Age profiling of fossil faunal samples relies on the correlation of animal tooth-wear patterns with life history stages, but the criteria used to infer these stages are not necessarily valid. Here we redefine some commonly used prey age classes, such as “juvenile,” “prime-age adult,” and “old adult,” based on the variable characteristics of tooth wear that we have observed in different ungulate size classes, and argue that prey vulnerability to predation is not so clearly predicted by the simplified age classes in widespread use by zooarchaeologists. We recommend instead classifying the youngest animal remains as either *young juvenile* or *subadult juvenile*, and adult remains as *early prime*, *late prime* or *old*, and provide specific criteria of dental eruption and occlusal wear for making these determinations. We argue this refined age profiling system, when used in combination with other types of zooarchaeological and taphonomic data, can provide accurate inferences of faunal accumulation processes.

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Introduction

Age–frequency distributions, or mortality profiles, of prey animals are common and potentially powerful analytical tools in the paleontological sciences. Paleoanthropologists, specifically, use mortality data to address research questions about early hominin prey acquisition strategies (e.g., hunting or scavenging), prey selectivity, and seasonality. In the course of our research on bovid mortality patterns in the ca. 1.8 million year old (Ma) fauna from the site of FLK 22 *Zinjanthropus* (Olduvai Gorge, Tanzania) (Bunn and Pickering, 2010) we identified critical areas in which methodology might be improved to bring paleoanthropological studies of ungulate mortality closer to the scientific realism of the past. In this paper, we describe methodological adjustments that address these shortcomings, which will, hopefully, lead to more realistic models of early hominin foraging behavior.

Analytical approaches in paleoanthropological studies of ungulate mortality

Regularities in the age structure of living populations of animals are well known and provide a baseline for comparisons between mortality samples from living populations, where direct observation can establish cause-and-effect relationships, and mortality samples from the archaeological and fossil records, where cause-and-effect

relationships must be inferred (e.g., Voorhies, 1969; Schaller, 1972; Kruuk, 1972; Frison, 1978; Klein, 1978; Stiner, 1990, 1991; Lyman, 1994; Steele, 2002; Steele and Weaver, 2002). In both present and ancient contexts, dental evidence enables estimation of each animal's age at death using some combination of three techniques: tooth eruption and occlusal wear description; crown height measurement; cementum increment analysis.

When the resulting mortality profile of a tooth sample is depicted graphically (as histograms or frequency polygons with advancing age on the *x*-axis and frequency on the *y*-axis), strong resemblance to a stable living population indicates a cause of death that was non-selective with respect to age or physical condition and is commonly labeled a mass death, catastrophic, or living structure profile (Fig. 1). If, instead, a mortality profile contrasts with a living population and exhibits an abundance of the weaker young and old individuals, as opposed to the physically prime adults which are abundant in a living population, then the profile is labeled attritional (Fig. 1). Yet another profile exhibiting strong selection for prime adults is labeled prime-dominated by Stiner (1990), who attributes the profile exclusively to hunting by hominins (Fig. 1). A familiar zooarchaeological example of the histogram approach is Klein's (1978, 1999) study of the Middle Stone Age (MSA) site of Klasies River Mouth (KRM, South Africa), in which he contrasted catastrophic and attritional profiles and hominin hunting of eland (*Taurotragus oryx*) and African buffalo (*Syncerus caffer*), respectively.

More recently, Stiner (e.g., 1990) grouped ungulate mortality data according to three meaningful life-history stages (juvenile, prime adult, old adult) recognized from wildlife ecology. She divided mortality data from published wildlife studies and from Italian Middle

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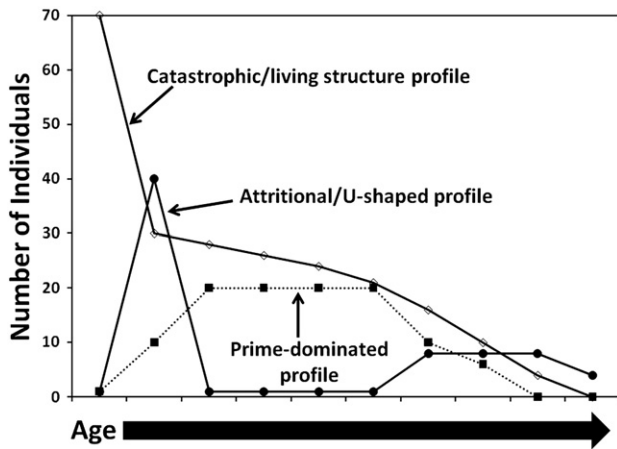


Figure 1. Schematic catastrophic, attritional, and prime-dominated age/mortality profiles.

Paleolithic sites analyzed by her into these juvenile, prime, and old groups, converted the data to percentages for each mortality sample, and plotted each sample as a discrete point on a triangular graph. This methodological advance facilitated visual comparisons of many mortality samples on a single graph. For example, one of them showed a clear distinction between prey mortality caused by cursorial predators, such as cheetahs (*Acinonyx jubatus*), hyenas (*Crocuta crocuta*, *Hyaena brunnea*), and African wild dogs (*Lycaon pictus*) versus mortality profiles created by ambush predators, such as lions (*Panthera leo*) and leopards (*P. pardus*) (Fig. 2). The former group of predators preferentially kills juveniles and old prey, producing attritional profiles, while the latter group is non-selective with respect to prey age, producing catastrophic, living structure profiles, as described in the wildlife literature (e.g., Schaller, 1972; FitzGibbon and Lazarus, 1995).

Steele and Weaver (2002) recognized that the original triangular graph approach compared very different sizes of mortality sample without controlling for these differences. To deal with this limitation they developed computer software that uses bootstrapping statistics to produce a density contour around each graphed sample point that was sensitive to sample size and approximated a 95% confidence interval. Small samples produced large density contours, and vice versa. Thus, graphed mortality samples whose density contours do not overlap were probably generated by different causes, at a 95%

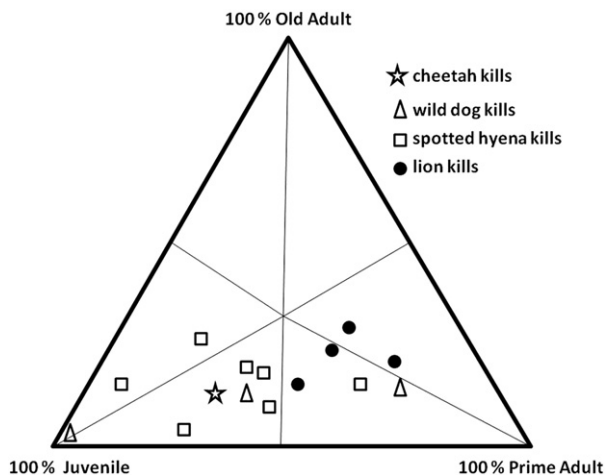


Figure 2. Triangular graph with some African carnivore-kill data. Adapted from Stiner (1990: Figure 8).

confidence level; samples with overlapping density contours cannot be distinguished at that statistically significant level.

Recommendations for resolving intrataxonomic disparities between prey life history stages and behavioral capabilities

Obviously, paleoanthropologists strive to define analytical age/mortality classes in ways that provide the best possible match between the criteria of tooth eruption and wear commonly used in wildlife and fossil research, and the research question(s) about hominin behavior they are investigating. However, in previous studies of hominin hunting capability, various researchers have consistently committed a fundamental error in defining those analytical age/mortality classes by reference to physiological life events, such as onset of female reproductive decline, or the behavioral shift in residence in males from mixed breeding herds to smaller, bachelor herds or more isolated existence, to characterize the transition of adults from prime to “past prime” (Schaller, 1972) or generally older status. While heuristically expedient, we argue that the underlying logic of this approach is essentially flawed since major life history events rarely coincide exactly with complete diminishment of the behavioral capabilities of potential ungulate prey, including the ability to elude or successfully counterattack a predator. In this section we provide details of the problem and offer methodological adjustments to overcome it.

Young animals

The end of the juvenile stage, as defined dentally, is clear: the loss of all deciduous teeth and the presence of all permanent teeth in occlusal wear mark this threshold. Commonly spanning approximately the first 20% of potential ecological longevity (PEL), or lifespan, in large ungulates, the juvenile stage is reasonably divisible into a *young juvenile* (newborn through yearling) substage and a *subadult juvenile* substage (Fig. 3). We suggest, except perhaps in circumstances of extraordinary preservation, that paleoanthropological analyses of ungulate mortality be restricted to *subadult juveniles*. Excluding *young juvenile* animals avoids a mismatch between modern African carnivore kill data, in which babies are abundant, and fossil assemblages, in which fragile bones of babies are usually uncommon, probably as a result of severe biostratigraphic and diagenetic bias against preservation of such fragile elements (e.g., Munson, 2000; Munson and Garniewicz, 2003). Because variants of the hominin hunting hypotheses that view humans as mighty hunters are not founded on the capture and bashing of small, often immobile, naïve babies, an analytical focus on the older, *subadult juveniles* that approach adults in size and physical strength, along with the *prime* and *old adults* themselves, is appropriate.

Bovids classified as *young juveniles* possess lightly to moderately worn deciduous premolars and erupting M_1 and M_2 . Those classified as *subadult juveniles* have moderately to heavily worn or shed deciduous premolars and erupting/erupted permanent premolars and molars. We illustrate the result of excluding *young juveniles* from comparative analyses; in general, this procedure reduces the apparent numbers of young individuals, thus skewing mortality patterns toward adult predominance (Figs. 4 and 5). There may be a reluctance to narrow the database in this way on the argument that analytical use of all of the available mortality evidence must be better. By that reasoning, analysis comparing fossil and modern mortality data proceeds either by assuming that the data from the different contexts match adequately to warrant comparison, or by adjusting the fossil profile to conform better to a modern or idealized pattern.

An example of the latter is Klein's (1978, 1999) analysis of the eland mortality data from KRM. Klein's analysis revealed many prime adult eland but few baby (or *young juvenile*) eland. Klein suggested that the “missing” *young juvenile* eland bones, owing to their fragility, had been lost postdepositionally, which, he argued, warranted

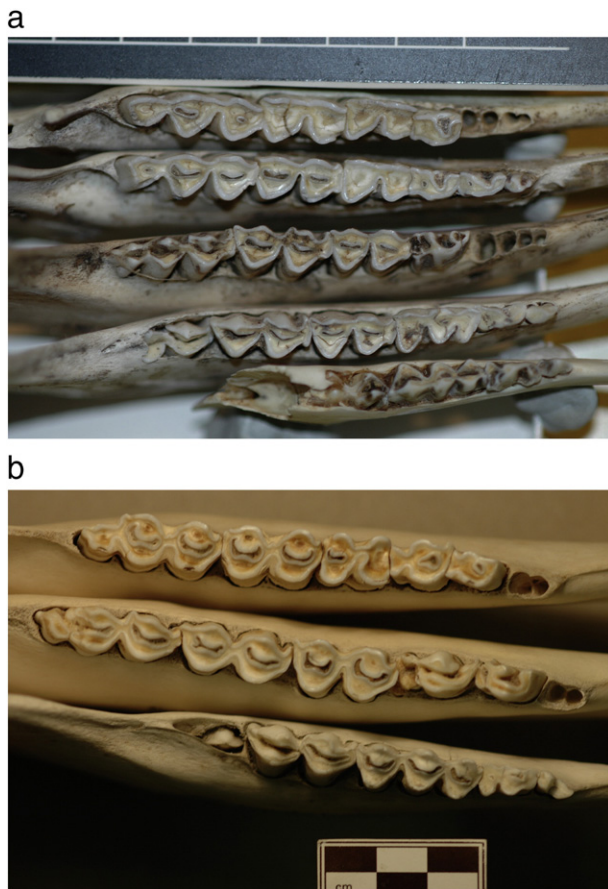


Figure 3. Occlusal views of size group 1 Thomson's gazelle (*Gazella thomsoni*) (a) and size group 3 red hartebeest (*Alcelaphus buselaphus*) (b) hemimandibles, illustrating age classes proposed here. From bottom to top, the Thomson's gazelle specimens derive from a *young juvenile* (with moderately worn deciduous premolars and an erupting M_1), *subadult juvenile* (with well-worn deciduous premolars and an erupting M_3), *early prime adult* (with its full permanent dentition moderately worn, but no infundibulum loss), *late prime adult* (with substantial wear on its full permanent dentition, including loss of the mesial and distal infundibula on M_1) and *old adult* (with loss of all infundibula on M_1 and M_2). From bottom to top, the red hartebeest specimens derive from a *young juvenile*, *early prime adult* and *old adult*. Note that the smaller Thomson's gazelle *late prime adult* specimen shows more advanced occlusal wear than does the larger *late prime adult* red hartebeest (see text for detailed discussion of this topic).

projecting them back into the mortality profile. Doing so created an eland mortality profile that resembles an idealized catastrophic pattern, and led to Klein's behavioral interpretation of hominin hunters driving eland herds over cliffs. Not projecting in any "missing" *young juveniles* into the eland profile makes the profile appear more prime-dominated, as in selective hunting of prime adult eland. In many bovid species, *subadult juveniles* (which are abundant in the KRM eland sample) approach adult size, observe the same herd behavior as their mothers, and are not easy prey.

Older animals

Another recommended methodological adjustment involves the age threshold between *prime* and *old adults*, and, thus, the definition of these two age classes (Fig. 3). The age (expressed as percentage of PEL) at which such life-history transitions from *prime* to *old* status occur varies intra- and interspecifically by sex, and any corresponding change in vulnerability to predation is also differential. We discuss interspecific disparities in the next section of this paper, concentrating

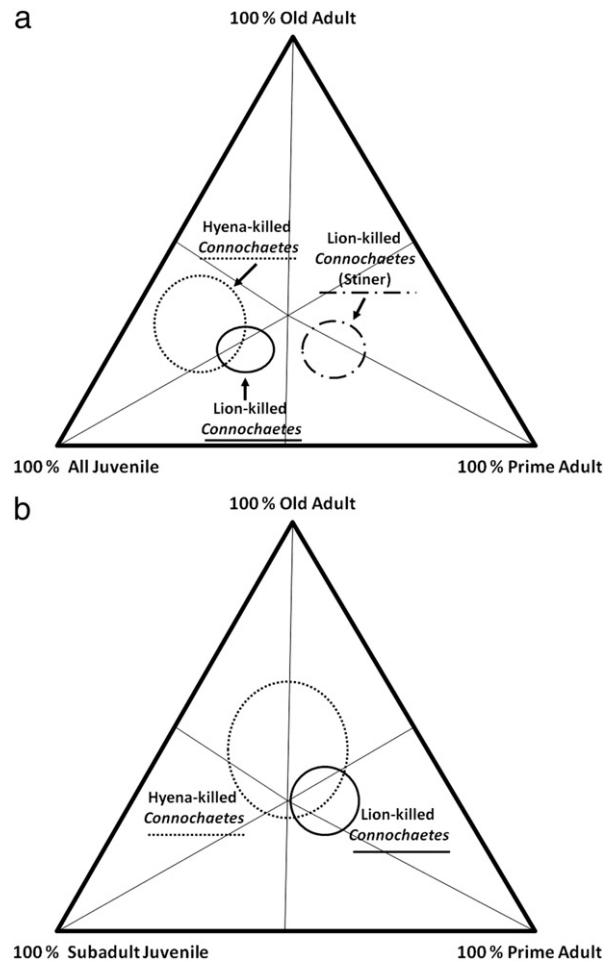


Figure 4. Modified triangular graphs of Serengeti hyena-killed and lion-killed wildebeest, including (a) and excluding (b) *young juvenile* (see text for definitions of age categories) wildebeest. Stiner (1990) analyzed *subadult juveniles* in Schaller's (1972: 438–439) lion-killed wildebeest data as *prime adults*, which is understandable, given Schaller's presentation there, but incorrect. *Subadult juvenile* wildebeest (Schaller's age class V) are "two-year-olds" and exhibit deciduous premolars and unerupted or partially erupted permanent premolars and M_3 ; the full permanent dentition and *prime adult* status is achieved at about 3.5 years of age (Schaller's age class VI). In Stiner's analysis (see Fig. 2, this paper), the effect of this was to over-emphasize *prime adults* at the expense of *juveniles*, which resulted in the plotting of lion kills in a similar position to leopard kills and in the recognition of an apparent distinction between the prey preferences of ambush predators (lions and leopards) and cursorial predators (spotted hyenas). Replotting Schaller's age class V wildebeest correctly as *juveniles*, or as *subadult juveniles*, eliminates the visual and the statistical distinction at the 95% confidence level, in the Serengeti wildebeest mortality data from cursorial hunting by spotted hyenas and ambush hunting by lions. Although statistically indistinct, lions do seem to kill a higher proportion of *prime adult* wildebeest than do spotted hyenas.

here on intraspecific implications of *prime-old* life history transitions contrasted with the actual behavioral capabilities of *old* individuals.

There are two relevant and fundamental questions that frame consideration of any specific dataset dealing with these later-stage portions of prey life history. First, does a premature age estimate of the *prime-old* thresholds correspond to an elevated risk of predation for an individual ungulate? Because of behavioral shifts in resident groups and in resident habitat preference that recur in multiple bovid species, the general answer is yes (Sinclair, 1977). Smaller group size, physical position within herds, and/or residence in habitats with increased bush-woodland vegetation increase vulnerability to predation by large felids, and in principle, this might have a similar effect regarding predation by hominins.

Second, from the perspective of hominin hunting, what would an abundance of individuals in a mortality sample that were just older

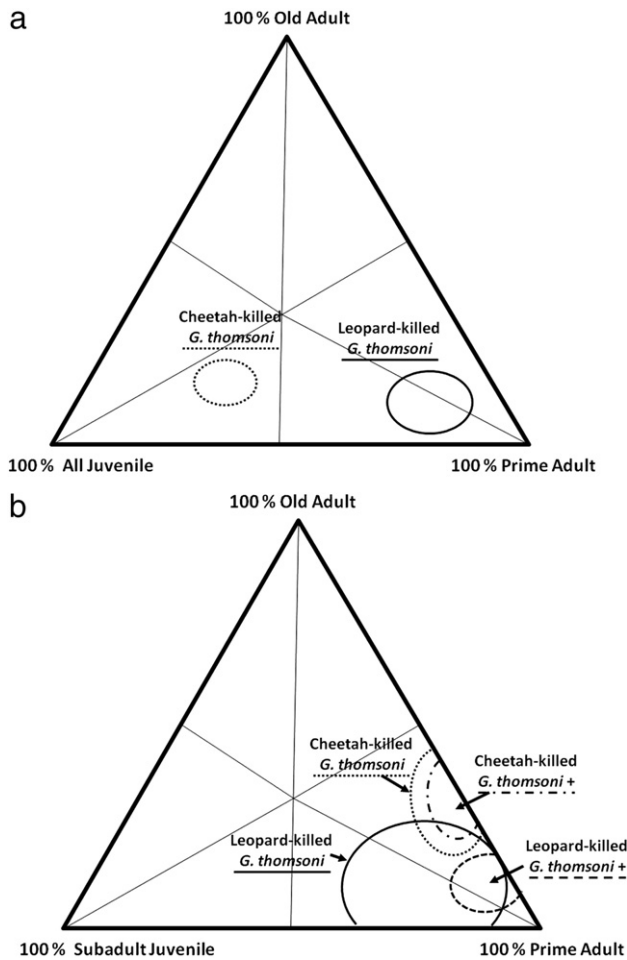


Figure 5. Modified triangular graphs of Serengeti leopard-killed and cheetah-killed Thomson's gazelle, including (a) and excluding (b) *young juvenile* gazelles. Data are reported in Schaller (1972). Schaller's observations include age-class data for 30 leopard-killed and 192 cheetah-killed gazelles, shown here in (a). Schaller reported an additional unaged-adult sample of 58 leopard-killed and 36 cheetah-killed gazelles; these are assigned to age class according to the proportions of the smaller, observed sample and are shown in (b) as separate distributions (labeled leopard-killed *G. thomsoni* + and cheetah-killed *G. thomsoni* +).

than the early, *prime-old* threshold (i.e., just older than the 40%–50% of PEL in African buffalo,¹ or just older than 50%–65% in some other bovid taxa [see below]) signify in behavioral terms? According to Klein (e.g., 1978, 1999), it would mean that MSA hominin hunters avoided dangerous prime adult prey of aggressive taxa such as buffalo, and unlike their behaviorally modern counterparts in the Later Stone Age (LSA), were only capable of killing non-threatening young and old prey.

We argue, instead, that the same MSA hunters of buffalo (assuming Klein's hunting interpretation is correct) targeted the more vulnerable segment of the buffalo population, thereby practicing a strategy similar to lions (the alternative, of course, is that they scavenged from lions). We argue further that this does not mean that hominins were avoiding and incapable of hunting large, dangerous prey, as Klein reasons. This is because there are two behavioral questions involved, *hunting selectivity* and *hunting capability*, that were previously conflated but that actually warrant two separate evaluations. MSA hominins were evidently selective hunters who exhibited vigilance comparable to lions in

targeting the relatively more vulnerable, smaller social groups of adult buffalo. On the question of hunting capability, the same MSA hunters were also evidently capable of killing dangerous adult buffalo whose approximate age of 12–14 years equals 50–60% of PEL. We doubt whether buffalo of that age were, in any realistic sense, decrepit, easy prey just waiting to die, just as we doubt that being gored and trampled by one of them would differ significantly to a hunter from suffering the same fate from a 10- to 12 old (40–50% of PEL) buffalo. And while it is important to note that scavenging from lions is an alternative and complementary strategy that could yield the same bovid mortality pattern, it is equally relevant to highlight the broken quartzite “projectile point” tip found embedded in a buffalo cervical vertebra from KRM (Milo, 1998). In short, MSA hunters at KRM were capable of killing dangerous adult buffalo (for a related discussion of MSA hunting, see Faith, 2008). When using mortality data to evaluate hunting capability of hominin predators, assigning old age to a prey animal should convey the sense of a physically impaired, easy-to-kill individual, in contrast to a younger, physically robust, hard-to-kill or even dangerous individual; we develop this argument further below.

Assessing actualistic limitations and recommendations for resolving intertaxonomic variability in predators and prey

Recognition of variability in the expression of complex predator-prey dynamics at short-term archaeological sites is the key to evaluating Pleistocene mortality data. In the uniformitarianist sense of Simpson (1970), likely variability around a central tendency of any of the processes involved means that multiple case studies and large, representative samples are prerequisite for establishing that central tendency. For example, the prey preferences of large African felids are well documented in the elegant, carefully-detailed research by Schaller (1972) and others in the Serengeti (e.g., Sinclair, 1979; Caro, 1994; Sinclair and Arcese, 1995), and the mortality profiles that they tend to produce in large samples of their prey have been illustrated for lions and leopards (living structure profiles from ambush hunting), and for cheetahs (attritional profile from cursorial hunting) (Fig. 2).

We do not mean to imply, however, that large carnivores in the Serengeti are either rigid or highly selective (relative to living prey populations) in their predation; indeed, wildlife researchers themselves are reluctant to do so in the absence of more complete data (e.g., Schaller, 1972; FitzGibbon and Lazarus, 1995). Using those mortality profiles as the basis for precise interpretations of Pleistocene dynamics, requires the bridging, uniformitarianist assumptions that directly ancestral felids of the Pleistocene practiced the same prey preferences, and that the prey populations also had the same paleo-age structure during the Pleistocene time interval sampled at the particular site. If, in the years preceding that sample, there occurred some phenomenon causing instability in the prey population, some attritional (e.g., disease or drought) removal of weaker young and old individuals, for example, then a subsequent living-structure sample would appear more prime-dominated. Other hypothetical scenarios influencing age structure of prey could easily be envisioned.

Likewise, and despite all of the careful, long-term wildlife research that has been accomplished, significant limitations in knowledge remain in key areas, including: carnivore prey preferences in a greater variety of ecological settings; sample sizes for many bovid prey species; tighter control over the relationship between dental attrition and ontogenetic age for a greater range of ungulate taxa. The latter gap in our understanding has exerted profound influence in interpretations of early hominin hunting capabilities.

In the best published example, Klein's (e.g., 1978, 1999) studies of faunas from KRM and from many other southern African sites derived interpretive leverage from Sinclair's research on African buffalo, by adopting the 40–50% PEL threshold as the boundary between *prime*

¹ In well-known, classic studies of African buffalo, Sinclair (1977) documented the residential shift of male buffalo out of mixed breeding herds at the fairly young age of 10–12 years (or about 40–50% of PEL of 24 years), which he correlated with increased vulnerability to lion predation and increased mortality in males, but not females, at that age.

and *old age*, not only in buffalo but also in most other African ungulates, and by assuming that “longevity is very similar among closely related species of similar size” (Klein and Cruz-Uribe, 1984: 50). From this basic assumption Klein interpreted the KRM bovid mortality data to hypothesize that MSA hunters there killed prime adults of relatively docile eland but restricted predation on buffalo to the very young and the old/very old, while avoiding “dangerous” prime adults of buffalo and other aggressive taxa. In contrast, Klein argued that more recent, behaviorally modern hunters in the LSA in the same region were more capable hunters of dangerous prime adults of buffalo and other aggressive taxa. Other archaeological researchers analyzing mortality data have tended to follow Klein's precedent of employing an early onset of old age of approximately 50%–65% of PEL in large ungulates in analyzing mortality data from their archaeological sites.

We believe that Klein's simplifying assumption based on the ontogeny of African buffalo surrenders much of the interpretive potential of ancient mortality data from many contexts. Seeking greater behavioral resolution in the development of working hypotheses should be a priority, which can be achieved by a broader, more flexible definition of the *prime adult* (and other) age classes. We, thus, view the *prime adult* age class in an expanded way, and we define transitions within it using criteria of dental attrition, cementum increments, and percentage of PEL. From this perspective, *prime adulthood* extends from the end of the *subadult juvenile* stage (see above) to the onset of obvious old age in the sense of physical infirmity and dental exhaustion (~75% of PEL). We divide *prime adult* bovids into two age classes: *early prime*, from ~20% to 50% of PEL (following Klein), and *late prime*, from ~50% to 75% of PEL, which places into the *old adult* class (or at least at the *late prime-old* boundary), the “past prime” grouping of Serengeti wildebeest and other uncommon taxa of Schaller (1972). As we have argued, “past prime” wildebeest (and other bovids) seem likely to still be quite viable physically, even if behaviorally, by isolating themselves, they are exposed to greater risk of predation.

It is a challenge to match these approximate boundaries between age classes with characteristics of dental attrition. A potentially useful characteristic that is commonly used in both wildlife and paleontological studies is the progressive loss of molar infundibula, starting with the mesial infundibulum on M_1 and continuing distally. As typically the first infundibulum to be worn away, the mesial infundibulum on M_1 is a convenient landmark that would seem to warrant further consideration for possible correlation with ontogenetic age and percentage of PEL. However, the loss of the mesial infundibulum from M_1 (and the progressive loss of others) does not correspond to a single percentage of PEL across all bovid taxa and size groups. Unsurprisingly, there is considerable intraspecific variation within local populations and across wider ranges, owing to such factors as diet and the effect of local substrate (ingested grit) on rates of dental attrition (e.g., Attwell, 1980; Attwell and Jeffery, 1981; Jeffery and Hanks, 1981).

That said, the timing of infundibular loss does, however, appear to be reasonably consistent within bovid size groups (see Brain, 1974, 1981; 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), at least at a low level of resolution sufficient to identify broad age classes, when we compare available data on common taxa, which we illustrate first for size group 3 (250–750 lbs.). For wildebeest (*Connochaetes taurinus*) in the Serengeti, Schaller (1972) used the loss of the mesial infundibulum on M_1 to categorize individuals as “past prime” (not “old”, which involved the loss of both infundibula on M_1 and M_2). When Sinclair (1977: 307, Table 8) analyzed Schaller's data, presumably from cementum increments on the actual mandibular teeth, he reported an age of 13–15 years for Schaller's “past prime” wildebeest. In other words, the loss of the mesial infundibulum in M_1 of Serengeti wildebeest occurs between ages 13 and 15 years, or at least 72% and up to 83% of a PEL of 18 years.

In contrast, Blumenschine (1991) used the same dental characteristic, loss of mesial infundibulum in M_1 , to identify “old” wildebeest in the Serengeti, which he estimated incorrectly to have reached only 55.6% of PEL, without citing Sinclair's (1977) earlier research on Serengeti wildebeest, by extrapolating from an independent study by Attwell (1980) of wildebeest in South Africa. For waterbuck (*Kobus ellipsiprymnus*), Spinage (1967) illustrates the loss of the mesial infundibulum from M_1 of heavily worn upper dentitions by 11 years. Assuming a typical bovid pattern of slightly more advanced wear on lower molars, a reasonable estimate of the age of loss of the mesial infundibulum from M_1 in waterbuck would be 9 or 10 years, i.e., similar to Serengeti wildebeest in view of the shorter longevity of waterbuck.²

For eland, a size group 4 bovid (750–2000 lbs), results are similar, although studies of wild populations do rely on analyses of small samples. In a study of dental attrition and cementum ages, Attwell and Jeffery (1981) divided 34 eland mandibles into 11 age classes. The M_1 was heavily worn with the loss of both infundibula by an average age of 10.5 years, which Attwell and Jeffery considered the onset of their “old” class (which was followed by an even older “senescent” class, comparable to *old* in the present study). Using their oldest individual (15.5 years) as the basis for PEL yields an estimate of 68% of PEL for the loss of both M_1 infundibula in eland. Klein and Cruz-Uribe (1984), in contrast, favor a PEL value of 20 years for eland, but that seems to be based on captive eland in domestication projects (Mentis, 1972). So, even though the resolution of available data is not high, the larger bovids of size groups 3 and 4 discussed here exhibit a loss of the mesial infundibulum from M_1 at an approximate percentage of PEL in the mid-60% to high-70% range, which contrasts with the significantly earlier stage of life of smaller bovids when this same dental characteristic is attained.

Available data on smaller bovids of size groups 1 and 2 (10–50 lbs and 50–250 lbs, respectively) indicate rapid, early loss of the mesial infundibulum of M_1 within the *early prime* adult class. Spinage (1971) reports loss of the mesial infundibulum of M_1 by an age of 4 years (~33% of a PEL of 12 years) for impala (*Aepyceros melampus*), which he attributes to an initial shallowness of that infundibulum and biomechanical factors. He cites the loss of the mesial infundibulum from lower M_2 at ~7 years. Starting at ~7.5 years (~62% of PEL) and continuing through the 9–12 years age of “senescence” (i.e., ~75%–100% of PEL), mandibular “infundibula of M_2 and M_3 [are] all, or almost all, absent.” Maxillary dental attrition lags behind mandibular attrition; for example, Spinage reports loss of the mesial infundibulum from M_1 at 7 years of age. For smaller Thomson's gazelle (*Gazella thomsoni*), in size group 1, Robinette and Archer (1971) report loss of the mesial infundibulum from M_1 at ~2–3 years of age (~27% of a PEL of 11 years). Although their methodology of counting the number of infundibula lost from the mandibular dentition and providing representative photographs differs from the approach of Schaller (1972: 441) and the present study of specifying particular infundibula as landmarks, there is reasonable agreement that both infundibula are lost from M_1 and M_2 at ~8 years of age (~73% of PEL) and that this marks the onset of *old age*. Several species of even smaller dik-diks (*Madoqua guentheri*, *M. saltiana*, and *M. kirkii*) exhibit similar or even more pronounced, rapid loss of molar infundibula (personal observations), which we suspect also relates to some combination of dental structure, local substrate, and diet, and which may limit the usefulness of molar infundibula for analytically grouping the very smallest sizes of bovids into the several adult age classes discussed here. For present purposes, we note that in some smaller, size groups 1–2 bovids, the loss of the mesial

² Mentis (1972) provides longevity data for waterbuck ranging from 13 to 16 years, but his samples are small and some are based on captive animals. Spinage's (1967) study of waterbuck revealed a maximum age of 11 years in males and 13 years in females, with one ($n = 1$) outlier at 18.5 years, based on cementum increments, which he discounts as representative of longevity in the wild.

infundibulum from M₁ occurs so early in adult life that this cannot be used as a landmark for the transition from *early prime* to *late prime* adulthood, for past prime age, or for the transition to *old* age, as it can be in the larger, size groups 3–4 bovinds discussed above.

An example of the ambiguity in correlating dental attrition rates and life history transitions in small bovinds—and then successfully applying those findings to the paleontological record—comes from our analysis of the klipspringer (*Oreotragus oreotragus*) and reedbuck (*Redunca* sp.) lower dentitions from Gondolin, a Pleistocene cave site in South Africa (see Bunn and Pickering, 2010). Two independent taphonomic studies of the Gondolin fauna concluded that the bovinds were collected predominantly by leopards or some other predator that behaved in a leopard-like way (Watson, 1993; Adams, 2006), but the mortality patterns of the smaller, size group 1 klipspringers and the larger, size group 2 reedbuck do not match (Table 1). The klipspringer lower molars are much more heavily worn than those of the reedbucks; we suspect that this disparity can, at least in part, be explained by the still poorly understood effect(s) of body/jaw/tooth size mentioned above.

Conclusions

When using mortality data to evaluate hunting capability of hominin predators, assigning *old age* to a prey animal should convey the sense of a physically impaired, easy-to-kill individual, in contrast to a younger, physically robust, hard-to-kill or even dangerous individual. The advanced occlusal wear defining the *late prime-old* boundary in this context is loss of the mesial infundibulum on the M₁ of some larger, size group 3 bovinds and of both mesial and distal infundibula on the M₂ of some smaller, size group 1–2 bovinds, which occurs relatively late in life in various bovinds, at ~75% of PEL (see below).

For addressing more detailed issues of hunting selectivity, the subdivided *prime adult* stage that we propose enables consideration of behavioral dynamics of predators and prey known from wildlife research. To describe the adult stage of life history, we advocate a flexible approach that can accommodate the overlapping research needs of paleontologists and archaeologists, whose evidence is teeth, and wildlife researchers, whose evidence is live animals. In addition to the two juvenile age classes (*young juvenile* and *subadult juvenile*), we recommend classifying adult animals into three age classes: (1) *early prime*, from ~20% to 50% of PEL (in some studies, this extends to ~60% of PEL), with full permanent dentition showing light to moderate and substantial occlusal wear but no loss of molar infundibula (this categorization applies to size group 3 bovinds, not to smaller taxa that start losing lower molar infundibula earlier in life); (2) *late prime*, from ~50% to 75% of PEL, with moderate and substantial occlusal wear but no loss of mesial infundibulum from M₁; (3) *old*, from ~75% to 100% of PEL, with heavy occlusal wear and loss of both mesial and distal infundibula from M₁ and M₂ (this categorization applies more widely across bovid size groups) (Fig. 3).

Researchers can group data in these age classes as desired to accommodate differing research needs. To minimize the chance of overemphasizing *prime adults* in our recent analyses of the FLK 22 *Zinjanthropus* and other early Pleistocene paleoanthropological faunas (Bunn and Pickering, 2010), we analyze fossil specimens essentially on the boundary between *late prime* and *old* age, as *old adults*, which conforms to Stiner's usage and places Schaller's "past prime" adults in the *old adult* class. Figures 4 and 5 use mortality data from modern carnivore kills in the Serengeti to illustrate how these redefined age classes focus attention away from the *young juveniles*, while still maintaining statistically significant distinctions between different carnivores and hunting methods.

At the opposite end of the life history span, we recommend the alternative of adjusting the modern comparative mortality sample being analyzed to match better with fossil profiles, by simply

removing from consideration taphonomically vulnerable *young juveniles* animals from both modern (where they are abundant) and fossil (where they tend to be uncommon) datasets. With age classes

Table 1

Dentition eruption/attrition scores for *Oreotragus oreotragus* (size group 1) and *Redunca* sp. (size group 2) hemimandibles from Gondolin, South Africa.^a

Taxon	Catalog	Side	dp ₄	P ₄	M ₁	M ₂	M ₃	Age
<i>Oreotragus</i>	G 660	R	—	m	m	m	++	Old
	G 2100	L	—	m	m	m	++	Old
	G 2376	L	+	—	w	m	m	Young juvenile
	G 4089	R	—	m	++	++	++	Old
	G 4093	R	—	m	m	++	++	Old
	G 4109	R	—	++	++	++	++	Old
	G 4940	L	—	++	++	++	++	Old
	G 4943	R	—	m	w	w	m	Young subadult
	G 5086	R	—	m	++	+	+	Late prime/Old
	G 5759	L	—	m	+	+	m	Late prime/Old
	G 5760	R	—	++	++	+	w	Late prime/Old
	G 5761	R	—	m	m	++	++	Old
	G 6672	R	—	++	++	++	++	Old
	G 7336	R	—	m	++	++	++	Old
	G 7357	L	—	m	++	++	m	Old
	G 10747	L	—	++	++	++	++	Old
	G 10866	L	+++	—	w	w	—	Young/subadult juvenile
G 12469	L	w	—	w	—	—	Young juvenile	
<i>Redunca</i>	G 667	L	—	w	w	w	w	Early prime
	G 1315	L	—	+	w	w	m	Early prime
	G 1378	L	—	m	w	w	m	Early prime
	G 2150	R	—	m	w	w	m	Subadult juvenile/ Early prime
	G 2443	R	—	w	w	w	w	Subadult juvenile
	G 2455	L	—	++	w	w	w	Early prime
	G 4635	R	—	w	w	w	w	Early prime
	G 4636	R	—	+	w	w	w	Early prime
	G 4662	R	—	w	w	m	m	Early prime
	G 5084	R	w	—	w	—	—	Young juvenile
	G 5085	R	—	w	w	w	w	Early prime
	G 5763	R	—	+	w	w	m	Early prime
	G 5793	R	—	m	w	w	m	Subadult juvenile/ Early prime
	G 7347	R	—	++	w	w	m	Early prime
	G 7731	R	—	w	w	w	w	Early prime
	G 9317	R	—	m	w	w	w	Early prime
	G 9822	R	—	w	w	w	w	Early prime
	G 9881	L	++	—	w	w	w	Subadult juvenile
	G 10194	R	—	+	w	m	m	Early prime
	G 10234	R	—	w	w	w	m	Early prime
G 10831	L	—	m	m	w	w	Early prime	
G 10863	L	w	—	w	—	—	Young juvenile	
G 10199	L	—	m	m	w	w	Early prime	
G 11662	L	m	m	w	w	—	Subadult juvenile	
G 11890	L	w	—	—	—	—	Young juvenile	
G 11961	L	—	m	w	w	m	Early prime	
G 12466	R	—	w	w	w	w	Early prime	

^a Each hemimandible represents a separate individual; there are no antimeres in the analyzed samples. Each tooth preserved in the hemimandible was scored using the code summarized below and a cumulative overall age was then assigned to the complete jaw specimen. Even though two independent taphonomic studies of the Gondolin fauna concluded that the bovinds were collected predominantly by leopards (and/or by another type (s) of predator behaving as do leopards) (Watson, 1993; Adams, 2006), note the striking contrast in age categories represented in the *Oreotragus* and *Redunca* samples. The former, smaller-sized taxon is represented by many presumably *old* (+ *late prime*) individuals (78%), while the latter, larger-sized taxon is represented only by younger age classes, especially *early prime*. More work must be conducted but we hypothesize that occlusal surface loss in smaller, size group 1 bovinds proceeds much more rapidly relative to potential ecological longevity than in larger bovinds, and thus physiologically and behaviorally *prime adults* of small bovinds might be misclassified as *old* in studies utilizing dental attrition. This is consistent with Spinage's (1971) observations of the initially shallower infundibula of impala (small size group 2) molars, which leads to their rapid loss; for further discussion, see also Attwell and Jeffery (1981). Codes: — = a shed dp₄ or permanent tooth not yet fully erupted; m = tooth missing as a result of vagary of preservation, not necessarily from lack of its development and eruption; w = occlusal wear of varying degrees, but no loss of infundibula; + = loss of mesial infundibulum on permanent molars or distal infundibulum on P₄; ++ = loss of mesial and distal infundibula for permanent molars (heavy wear) or mesial and middle infundibula for dp₄; +++ = loss of all three infundibula on dp₄.

reduced thereby to *subadult juveniles*, *prime adult* and *old adult*, the data points and distributions on a triangular graph shift away from the juvenile (now *subadult juvenile*) corner. This procedure yields overlapping density contours on modified triangular graphs of modern mortality data plotting different predation strategies (Figs. 4 and 5). The overlap is, however, minimal and we predict that enlarging actualistic samples (and thereby reducing the dimensions of density contours) will provide distinct, statistically significant separation between cursorial and ambush predation. We are initiating a new program of fieldwork in various East African and southern African ecosystems, sampling multiple carnivore taxa and prey species, to address this issue.

In the meantime, the methodological adjustments we recommend here already place a greater emphasis on the definition of the *prime adult* class and on the *prime-old adult* boundary than in previous research on mortality patterns in paleoanthropology. In earlier studies, it is this extended phase of bovid life history that has also been least carefully considered from the perspective that escape and defense capabilities of prey animals probably persist well into the *old adult* stage, long after easily observed physiological changes have occurred. Our final recommendation to paleoanthropologists is that they make efforts to observe prey animal behavior in as many contexts and as often as possible to gain a real appreciation of this principle. Far from being “tyrannical” (e.g., Wobst, 1978; Lieberman et al., 2007) or detrimental to the development of sound hypotheses of human evolution, research in the present is the most pragmatic and productive way to advance our understanding of past dynamics, hominin meat foraging included.

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