

Mary C. Stiner
Department of Anthropology,
University of Arizona,
Tucson, AZ 85721-0030,
U.S.A. E-mail:
mstiner@u.arizona.edu

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Mortality analysis of Pleistocene bears and its paleoanthropological relevance

Bear bones and Paleolithic stone artefacts often co-occur in Pleistocene cave deposits of Eurasia, raising the question of how these associations come about and the need for effective methods with which to obtain a clear answer. Building upon knowledge of modern bears, I present a method for testing two competing hypotheses about the causes of bear mortality in hibernation contexts. The first hypothesis proposes that age-dependent deaths resulted from non-violent causes (principally starvation), implying that bears' presence in a cave was not linked in time to human activities there. The second hypothesis proposes that random bear deaths in caves resulted from hunting by humans or other large predators, implying a temporal link between them; the expectation of a nonselective age pattern in this circumstance arises from the fact that the individual characters of hibernating bears are hidden from predators. Three elements of the method and its development are presented: (1) a brief review of the biological bases of hibernation-related mortality in modern *Ursus*, its paleontological consequences, and test expectations drawn therefrom; (2) a detailed, illustrated technique for age-scoring isolated bear cheek teeth based on tooth eruption-wear sequences, developed primarily for cave and brown bears; and, (3) a simple, accurate way to evaluate real cases in terms of contrasting mortality models. The final step is demonstrated by application to a Middle Pleistocene cave bear assemblage (*Ursus deningeri*) from Yarimburgaz Cave in Turkey, a large collection found in general stratigraphic association with Paleolithic artefacts. The advantages of the method include its ability to (a) handle small samples, (b) use isolated tooth specimens, and (c) evaluate cases simultaneously in terms of idealized age structure models and the variation that normally is associated with each under natural conditions. While the more obvious benefit of bear mortality analysis may be to research on ancient bear demography, the principles and procedures offered here are equally pertinent to archaeological studies of carnivore-mediated formation processes in cave sites. As is generally true in taphonomic research, however, bear mortality patterns are most effective when used in combination with independent lines of evidence to address questions about assemblage formation.

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Introduction

Bear skeletal remains are encountered with great regularity in Pleistocene cave faunas of Eurasia, including many Paleolithic archaeological sites (e.g., Baryshnikov, 1997; Chauvet *et al.*, 1996; Gargett, 1996; Jenkinson, 1984; Kurtén, 1976; Pratt, 1988; Stiner, 1994; Stiner *et al.*, 1996). The pres-

ence of bear skulls and postcrania in shelter sites—sometimes in association with stone tools, other times not—has been taken by some as evidence of archaic human hunting, magic, or ritual behavior, interpretations inspired in part by the prominence of bears in the iconographies of some Holocene human cultures. Scenarios of Neandertal “cave bear cults”, and forced eviction by

spearpoint of giant bears from cave men's homes, continue to hold tremendous popular appeal. Yet claims for evidence of archaic human rituals, in which bear skulls (Bächler, 1940, 1957 cited in Kurtén 1976), deer antlers (Blanc, 1958, 1961; Piperno, 1976–77), or certain other non-human skeletal materials are cited as central props or symbols, are highly problematic (Binford, 1981; Chase & Dibble, 1987; Gamble, 1986; Kurtén, 1958, 1976; Spahni, 1954; Stiner, 1991, 1994; White & Toth, 1991). Cases dating to the dawn of the human species, well before any unequivocal form of art is preserved in archaeological records, are notoriously difficult to verify. There is surprisingly little evidence of direct interaction between early humans and bears overall.

Archaeologists must admit, however, that their abilities to falsify fanciful scenarios about archaic human behavior remain underdeveloped. Bear-artefact associations in Pleistocene caves are points of special contention. On the one side, doubters note that the bones of cave and brown bears in Paleolithic shelter sites seldom are marred by stone tools. Indeed, many professionals are now convinced that bear remains in Paleolithic cave sites most likely represent hibernation-related deaths that occurred independently of human uses of the same localities. Kurtén's (e.g., 1958, 1976) investigations have been particularly influential in this regard, due to his effective use of reference data on modern ursids and innovative analyses of paleontological samples. Taphonomic work on other Pleistocene cases (e.g., Brain, 1981; Jenkinson, 1984; Stiner, 1994; Stiner *et al.*, 1996) also demonstrates that the tempos at which geological and biological materials accumulate in caves can be quite different. Where cave sediments accumulate slowly, diverse biological and non-biological agencies may contribute materials to a single geological stratum. This is why so many cave faunas represent palimpsests or

“overlays” of multiple bone accumulation events, such as in Yarımburgaz Cave in northwest Turkey (Stiner *et al.*, 1996), selected data on which are presented below.

On the other hand, a number of observations can be marshaled in favor of direct interactions between Pleistocene humans and bears, or at least isolate weaknesses in the opposing view. It is generally known, after all, that humans can in some circumstances process game without leaving traces of tool marks on prey skeletons (e.g., Lyman, 1994), and occasional predation on hibernating bears by humans is widely documented among modern traditional cultures where these species' geographic ranges overlap (e.g., Rogers, 1981:69; Ross *et al.*, 1988). Tool marks occasionally have been found on bear bones in a few Paleolithic cases dating to the Middle Paleolithic and onward (e.g., Bárta, 1989; Stiner 1994:109ff). Hence, it continues to be difficult to distinguish hominids' foraging refuse in cave sites from non-anthropogenic faunal components, even if we are confident about how such processes may operate in principle. Obviously, some clear-cut negation strategy is required on a case by case basis.

There are numerous benefits to learning why bears are common in Paleolithic cave sites, even if the conclusion proves to be that bears avoided humans as best they could when selecting winter beds. Knowledge about the occupation intervals of bears and humans in caves, for example, helps describe the ecological conditions under which human visits took place. Bear mortality patterns represent one independent and potentially pivotal line of evidence of bear denning (hibernation) behavior (Andrews & Turner, 1992; Baryshnikov, 1997; Gargett, 1996; Kurtén, 1958, 1976; Stiner, 1994; Stiner *et al.*, 1996), a potential explanation of why Pleistocene bear bones occur in caves, sometimes in great numbers. Left open, however, is the question of *how* bears die in Paleolithic caves. Hinging on

this question are interpretations of direct physical contact versus indirect ecological interactions between humans and bears, and, in some cases, whether unusual manipulation of skeletal materials by archaic humans took place.

Reported here is a method for analyzing the age structures of bear death assemblages, designed to address the question of whether Pleistocene bear remains found in caves represent hibernation-related deaths arising from non-violent (predator-independent) or violent (predator-dependent) causes. The first of these alternatives argues for temporal independence of bear and human components in caves. Because it represents the most likely non-anthropological explanation in these circumstances, it must be excluded before anthropological explanations may be forwarded. Of course, bear mortality data are most valuable to research on site formation histories if used in conjunction with independent lines of taphonomic evidence such as vertebrate species profiles, bear body part representation, and bone damage patterns (e.g., Gargett, 1996; Stiner *et al.*, 1996; Wolverson, 1996): a preponderance of bears suggests a den accumulation, for example; whole skeletons of bears also argue for deaths *in situ*; and bone damage may reveal who, if anyone, gained from those deaths.

Several studies have documented how approximate age at death in bears may be inferred from the stages of dental development or occlusal wear (Dittrich, 1960; Kurtén, 1958, 1976; Marks & Erickson, 1966; Torres, 1988), as well as how the age structure of a bear death assemblage may be constructed from these observations (Andrews & Turner, 1992; Gargett, 1996; Kurtén, 1958). With the exception of Kurtén's (1958) life table analysis, which focuses on age-specific survivorship in extinct cave bears, none of these studies has taken what I consider to be the final steps

toward interpretation of bear mortality patterns. Clear, divisible test implications are essential for comparing subject cases against alternative age structure models, especially those representing common mortality factors in nature (*sensu* Caughley, 1966, 1977; Lyman, 1987; Stiner, 1990). Because some structural variation is typical of every model (Caughley, 1977), the possibility that a case resembles alternative models needs to be falsified.

Age structure models are narrow, static representations of what is actually a dynamic process. Conceiving of the models as "pattern families", based on empirically defined ranges of variation, is a simple way of coping with this shortcoming (Stiner, 1990, 1991, 1994). Both considerations—idealized structural models and the variation surrounding each—are needed to distinguish between conflicting interpretations of bear remains in cave sites, such as attritional mortality in hibernation dens arising from starvation and disease as opposed to the consequences of *in situ* predation (surprise attacks in dens) by Pleistocene humans, hyenas, wolves, and/or other bears.

Herein lie the main contributions of this study. The test expectations are of taphonomic and behavioral interest because they are explicit and founded on independently formulated demographic principles common to mammals. Additional benefits of the approach include its fully illustrated aging scheme, which coordinates the eruption and wear schedules for six different cheek teeth, and its ability to handle small samples effectively. The age classification technique is equally suited to samples consisting of isolated or articulated teeth. This presentation is slanted to archaeological research on site formation processes, but the approach is also of value to paleoecological studies of Pleistocene brown and cave bears.

In order to appreciate the clarity of the test expectations for bear mortality in

cave sites, it is necessary to begin with some demographic and reproductive characteristics that modern bears hold in common, but which may not be obvious to anthropologists. Development of the method therefore involves three steps that are pertinent to hypothesis formation, data collection, and interpretation of results. First to be explored are the causal relations among bear hibernation behavior, life history characteristics, and mortality in and around den localities. A common theme is evident in the biology of modern members of the genus *Ursus* (black bear, *U. americanus*; brown bear, *U. arctos*; polar bear, *U. maritimus*), suggesting that many of their reproductive and metabolic characteristics also apply to extinct Middle and Late Pleistocene cave bears [the chronospecies *Ursus (Spelearctos) deningeri* and *U. (S.) spelaeus*, as well as *U. (S.) rossicus*]. These universal characteristics therefore serve as the basis for a series of test expectations. Second, an age-scoring technique is presented, based on eruption and occlusal wear sequences for the six major cheek teeth of bears over the maximum potential lifespan. Finally, a means for evaluating observed mortality patterns in relation to classic demographic models and their associated ranges of variation is presented. This third step is illustrated by application to a real bear death assemblage found in geological association with Paleolithic stone tools in Yarimburgaz Cave. Results obtained for six types of cheek teeth are checked for levels of agreement in this context.

Bear mortality in hibernation contexts: test implications

Knowledge of hibernation behavior and its contingencies in modern bears permits development of expectations for age structure patterns arising in frequently used dens from attritional mortality and from *in situ*

predation. At issue are two questions: What fraction of individuals in a living population normally hibernate?—this serving as the model for random predation by den raiders. And which age groups are most commonly affected by hibernation-related mortality arising primarily from non-violent causes including starvation, disease, and senescence? It should be noted at the outset that modern bears are known to use natural shelters—including rock crevices, overhangs, and true caves—as hibernation dens if they are available. This behavior is especially common where bear habitats are associated with limestone karst systems (Clevenger, 1991; Judd *et al.*, 1986; Reynolds *et al.*, 1976; Rogers, 1981); well-drained localities hidden by tree cover and with moderately steep taluses are preferred. Den sites may be reused by bears, and permanent shelters are likely to attract different individuals over time.

Life history characteristics and hibernation

Hibernation by bears is a means for enduring the scarcity of plants, invertebrates, and small vertebrates in winter (e.g., Clevenger, *et al.*, 1992; Ewer, 1973; Garshelis & Pelton, 1980; Rogers, 1981, 1987; Tassi, 1983). Rather than depending on large game in seasons when other foods are no longer available, bears possess the metabolic option to drastically reduce their need for energy (Folk *et al.*, 1976; Hellgren *et al.*, 1990; Johnson & Pelton, 1980; Rogers, 1981; Watts & Jonkel, 1988; Watts *et al.*, 1987). The success of the hibernation strategy hinges, however, upon food availability during the previous warm season, especially autumn. Mortality in modern bears therefore tends to be cyclical, and mortality is especially high toward the end of the hibernation period in stressful years (Garshelis & Pelton, 1980; Kurtén, 1976; Rogers, 1981, 1987). Starvation is the most common cause of hibernation-related deaths in most study areas, especially for cubs and subadults

(Craighead *et al.*, 1976; Rogers 1987). Starving adults generally do not die in sleep: they awaken early if their energy stores are over-depleted and make short forays in search of easy food, using the den as a foraging hub (Rogers, 1987:24–25, 70). Bears may hang about the den for up to a month after first emergence, and unfortunate ones collapse and die in the vicinity.

Hibernation lairs are also birthing dens for pregnant females. Delayed implantation of fertilized zygotes in adult females permits spontaneous adjustments to food supply and synchronization of births to the hibernation schedule (Bunnell & Tait, 1981; Bronson, 1989; Ewer, 1973:298–300). Zygotes can be aborted at little biological cost if the female enters hibernation in poor condition. Delayed implantation also maximizes the development time available to healthy but naturally altricial young before abandoning the den in spring.

Reproducing females tend to den longer than other adults in a given population (Rogers, 1981). Cubs of both sexes will hibernate with their mothers each winter until she rejects their company, normally between the second and fourth year in brown bears. The duration of cub dependency also varies within and between populations as a function of foraging conditions. Cubs that are abandoned early may form sibling duos, inseparable until they reach 2.5 to 3 years of age (Glenn *et al.*, 1976), indirectly testifying to the hazards of early independence. The importance and duration of hibernation for adult males and barren females may be the same or less than that of reproducing females, depending on the severity of seasonal lows in plant and small animal productivity and whether non-reproducing bears can obtain a regular supply of meat from large game in winter (Johnson & Pelton, 1980; Rogers, 1987).

Key aspects of bear life history and winter torpor are remarkably similar among modern species of *Ursus*. Bunnell & Tait's

(1981) comparisons of black, brown, and polar bears reveal nearly analogous ages at first parturition (between 4–8 years for all), maximum potential lifespans (25–30 years, see also Craighead *et al.*, 1976; Glenn *et al.*, 1976), average birth intervals (2 to >3 years), and litter sizes (1–2 in most study areas). The cubs of brown and polar bears become self-sufficient between 1.5 and 4.5 years of age, black bears somewhat earlier (0.5 to 2.5 years) (Bunnell & Tait, 1981:82). Bears therefore are characterized by long lifespans, also relatively late sexual maturation, protracted reproductive cycles, and high survivorship rates in adulthood (Craighead *et al.*, 1976). Bears evidently can afford a low reproductive capacity because of their large body size, effective defenses against predators, high maternal competence, and occasionally cooperative cub care (cub switching) among neighboring mothers. The average reproductive rate reported for grizzly bears in the Yellowstone ecosystem by Craighead *et al.* (1976; see also Ewer, 1973), for example, is 0.658 per annum, meaning that even minor changes in reproductive rate can affect the potential for population growth or recovery; a 25 year old female may achieve roughly six full reproductive cycles over her reproductive career and, in that time, expect to produce about 13 cubs. Bears have among the lowest reproductive rates known among terrestrial mammals (Bunnell & Tait, 1981:77; Craighead *et al.*, 1976; Glenn *et al.*, 1976) and, for this reason, modern bears are very sensitive to over-exploitation by hunters. It therefore is not surprising that bear meat forms only an irregular source of food in any modern human economy.

The cave bear's apparently strong phylogenetic affinities to modern bears, along with their paleontological abundance in Pleistocene cave sediments, indicate that they too were hibernators (Andrews & Turner, 1992; Baryshnikov, 1997; Kurtén, 1958, 1976). Similarities in the hibernation

process and demography of modern black bears (*U. americanus*, Hellgren *et al.*, 1990; Garshelis & Pelton, 1980; Johnson & Pelton, 1980; Rogers, 1981, 1987) and brown bears (*U. arctos*, for southern European browns, see Clevenger, 1990, 1991; Clevenger *et al.*, 1987, 1988; Clevenger & Purroy, 1991; Tassi, 1983) therefore permit certain generalizations about all bears (Watts & Jonkel, 1988; Watts *et al.*, 1987; see also Hellgren *et al.*, 1990; Johnson & Pelton, 1980), including Holocene and Pleistocene brown and cave bears.

Food supply is arguably the most important limiter of bear population sizes in modern environments because it directly impacts birth rates. Maternal nutrition limits a females' reproductive rate both prior to zygote implantation and during infant development before and following birth (Bunnell & Tait, 1981:83–84; Craighead *et al.*, 1976:354; see also Picton & Knight, 1986). Mortality factors play a secondary role in bear population dynamics, largely because the death rate in adults is quite low prior to senescence. Mortality rates are substantially higher for cubs under 1.5 years of age, however: up to 38% of the litter may be lost during this time, but losses ranging from 0 and 15% are more typical (Glenn *et al.*, 1976:389). Many of these deaths occur in the vicinity of natal dens. Kurtén (1958:25–27) obtained similar estimates of post-partum juvenile mortality rates for Pleistocene cave bears from Odessa, along with an apparently low probability of death during the prime adult years. Because cave bears appear to have been highly dependent on seasonally available plant mast, based on studies of dental morphology and stable isotope analyses of tooth enamel (e.g., Kurtén, 1976; Baryshnikov, 1997; Stiner *et al.*, 1998), and omnivorous diets extend hibernation times for non-reproducing adults, one can expect relatively long hibernation periods for adults of both sexes. The net result

is a nearly equal probability for adults of both sexes perishing in dens (Stiner *et al.*, 1998).

In addition to non-violent causes of death, denning bears may be attacked by predators such as wolves, dogs, humans, or other bears. A bear becomes nearly helpless as it drops into a reduced metabolic state. It is for this reason that bears make considerable effort to keep their hibernation lairs secret (for black bears, see Garshelis & Pelton, 1980; Johnson & Pelton, 1980; Rogers, 1981, 1987; for brown bears see Clevenger, 1991; Miller, 1985; Peterson *et al.*, 1984:38; Rogers, 1987; Ross *et al.*, 1988). Any sign of disturbance at a potential winter lair site is enough to turn a bear away. Cannibalism within and between bear species at dens and elsewhere can be commonplace during lean years, or in regions where bear population densities are especially high (Mattson *et al.*, 1992; Ross *et al.*, 1988; Tietje *et al.*, 1986). From a taphonomic viewpoint it should be noted that both scavenging and predation of hibernating bears can result in gnawing damage to bones. Frail bears may trigger attacks by other predators, but the carcasses of already dead bears would likely be scavenged.

Hibernation dens clearly are magnets for annual mortality in bears. The circumstances of den use greatly enhance the probability that bear bones will become part of the paleontological records of natural shelters, especially if the shelter is frequented across generations. However, bears can die from more than one set of causes in hibernation contexts—essentially violent and nonviolent—even if nonviolent causes predominate in modern situations. The unique biology of bears brings about distinct mortality patterns in dens in predominantly violent and predominantly nonviolent situations. These distinct age structures have different implications for bears' connection to prehistoric human activities at the same sites.

Expectations for cumulative deaths in hibernation dens

In light of the information presented above, four facts about bear life history and foraging habits appear to be especially important for modeling expectations of cumulative mortality in hibernation contexts:

(1) Most bear deaths in hibernation dens are caused by starvation, disease, and old age.

(2) Bears produce very small litters per reproductive event.

(3) Cub mortality rates are moderate to high, whereas those for adults are quite low prior to senescence.

(4) Nearly the entire bear population (adults and juveniles) can be found in dens for substantial portions of each year if the bears are highly omnivorous, a qualification which almost certainly includes cave bears, most brown bears, and black bears. Polar bears are totally carnivorous, and they are the exception that proves the rule linking hibernation times, diet, and sex ratios in dens.

These observations lead to the prediction that young and very old adult bears should be preferentially represented in hibernation-related death assemblages where starvation, disease, and senescence are the primary mortality factors. Prime adult bears should be conspicuously under-represented because their survivorship is high prior to senescence. In histogram format, such a mortality pattern would display a bimodal, or U-shaped (concave), age distribution. When compared to the age structure of a living bear population (Figure 1), the mortality profile resulting from *normal non-violent attrition* (the NNVA model) is distinguished foremost by the near absence of prime-aged adults. In habitats where food supplies allow males to hibernate for less time, females may predominate among the adults that spend long periods in dens. The proportion of juveniles to adults also may be amplified slightly as a result, but not to a

great degree since bears produce cubs in low numbers over long intervals. For these reasons bear mortality patterns in dens should not usually result in a juvenile bias stronger than that predicted by the NNVA model, because the small litter sizes of bears damp this tendency relative to most other den-dependent Carnivora (cf. strong juvenile biases for wolves and hyenas, Stiner, 1994:316–331; see also Kurtén's general discussion, 1958:4–5).

The mortality pattern expected to result from non-violent deaths in dens (NNVA) contrasts with that from hunting of hibernating bears by predators. Surprise attacks on sleeping bears by modern wolves and humans are well known, though relatively uncommon (see references above); Pleistocene hyenas occasionally may have done the same when their distributions overlapped with those of bears. If the practice was more common in the past, the mortality pattern generated by repeated hunting of hibernating bears should be indifferent to the ages of the individuals occupying dens, simply because there is little opportunity to spook or survey individual vulnerability while hunting encrypted prey. Repeated predation on hibernating bears in a cave therefore should affect prime adults, old adults, infants, and adolescents randomly, emulating their natural proportions in the living population sequestered in dens each year. Here, then, is the alternative expectation, namely the *living structure* (LS) model.

Although cut marks on Pleistocene bear bones are relatively rare in archaeological sites overall, gnawing damage by large carnivores frequently is noted (Andrews & Turner, 1992; Baryshnikov, 1997; Gargett, 1996; Kurtén, 1976; Stiner *et al.*, 1996; see also Wolverton, 1996 for a Holocene example). These observations raise the question of how the bears died but do not necessarily answer it. Gnawing damage on bear remains—or cut marks in the case

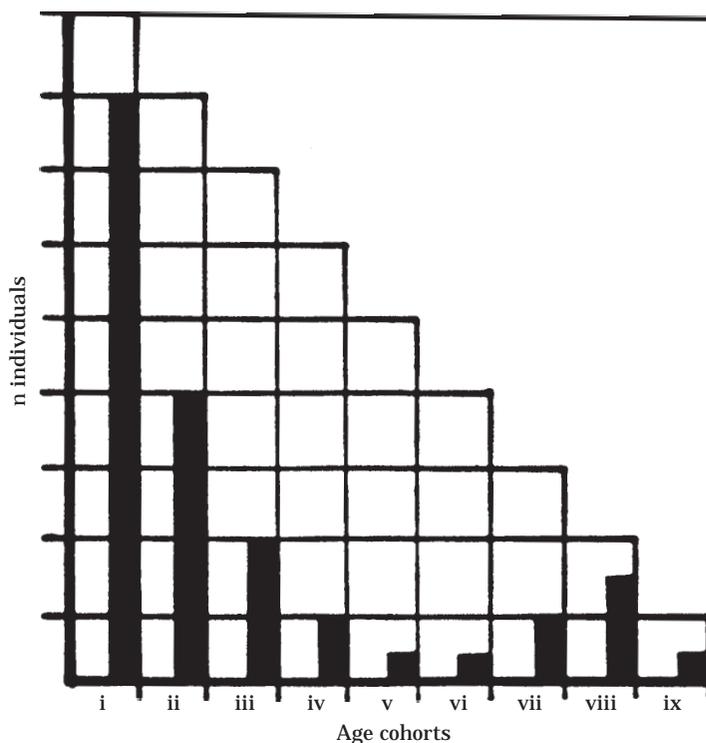


Figure 1. An idealized attritional (U-shaped or bimodal) mortality profile, indicated by vertical bars, superimposed upon the idealized model (grid) of the living population age structure. Under-representation of individuals in the prime adult age cohorts is the most important difference between the two idealized models. While a U-shaped mortality pattern can arise from non-violent causes or from open land predation by cursorial predators (see Stiner, 1990, 1994), only normal non-violent attrition (NNVA) applies in the case of hibernation-related deaths of bears. *In situ* predation on hibernating bears should instead affect individuals randomly with respect to age. *In situ* predation therefore should result in a death pattern that resembles the living age structure (LS) of the hibernating population, which in most bears closely resembles the structure of the entire living population. This kind of graphic representation does not, however, reflect the structural variation typically associated with either idealized model.

of human exploitation—is not proof of hunting, only consumption or related economic uses. It is the mortality pattern that potentially allows one to distinguish the circumstances of bone damage, specifically between hunting and scavenging contexts.

The age-scoring technique

This technique for constructing bear mortality patterns employs teeth exclusively, and it is suitable for age-scoring isolated specimens. Ideally, juveniles and adults also can

be distinguished on the basis of bone fusion (e.g., Marks & Erickson, 1966), but the taphonomic contexts of cave faunas, specifically the prevalence of gnawing damage by various large carnivores, often eclipses this possibility. The situation is different for dental remains, including deciduous teeth, providing that the enamel caps are nearly or fully formed at the time of death (following Wainwright *et al.*, 1976:223–224). Teeth present an additional advantage for age structure analyses in that they undergo continuous, highly diagnostic alterations over the complete lifetime, first

via development and later through occlusal wear of the crown.¹

In developing an eruption and wear scheme for bear teeth, it is relevant to note ursids' common adaptation to an omnivorous diet and the tendency for the occluding surfaces to be large in relation to crown height. The only exception to these generalizations is the recent dental specialization of the polar bear (*U. maritimus*). Pleistocene cave bears evolved toward another extreme, with massive, broad, multi-cusped dentitions for processing plant foods with tough stems and husks (Baryshnikov, 1997; Kurtén, 1958, 1976; Stiner *et al.*, 1998). Despite some dental variation among living and extinct bear species, the cheek teeth of all bears can be classified into consecutive age categories (stages) on the basis of crown and root development or, if mature, wear of occluding surfaces. Here I emphasize the status of permanent tooth crowns.

Figures 2 and 3 describe the age-scoring technique as a set of nine consecutive cohorts for upper and lower cheek teeth of bears. The scheme is developed foremost for cave bears but can be applied with minimal adjustments to other bear species, especially brown bears. Unlike any other age-scoring diagram published to date, the synchronized eruption and wear stages illustrated here are keyed to the quantitatively based age structure models and their respective test impli-

cations (see below). In this regard, it is analytically self-contained. This technique does not attempt, however, to estimate age in real years for any age stage, nor does it assume that the stages represent equivalent spans of time, as neither is really possible for prehistoric populations on the basis of eruption and wear observations. The scheme registers change in wear status on an ordinal scale.

The age-scoring technique was developed with the benefit of relatively complete maxillae and mandibles of cave and brown bears from Middle Pleistocene levels of Yarımburgaz Cave in Turkey, and from Upper Pleistocene levels in Buca della Iena, Grotta del Fossellone, Grotta dei Moscerini, and Grotta di Sant'Agostino in Italy (Stiner, 1994). The paleontological observations are supplemented by dental development data on modern brown and black bears (Dittrich, 1960; Marks & Erickson, 1966; Torres, 1988). The age-scoring technique emphasizes the molars and, to a lesser extent, the upper fourth premolar. Canines are not considered because their patterns of wear and damage were found to be very irregular in the Pleistocene reference collections (Stiner *et al.*, 1998; for other cases see Koby, 1940, 1953), and among some modern brown bears (Clevenger, personal communication, 1994). Moreover, permanent canines emerge late in the development sequence (Marks & Erickson, 1966; Dittrich, 1960), and the deciduous elements that precede them generally do not register much in the way of measurable wear (but see Andrews & Turner, 1992).

An important parameter for the eruption-wear scheme is the maximum potential lifespan (MPL). As noted above, the MPL cannot be determined in real years on the basis of occlusal wear for paleontological populations. Instead, complete destruction of cheek tooth crowns, especially those situated in the area of maximum wear, signals the end of the MPL on grounds that the

¹Ways of age-scoring teeth of modern and well preserved fossil populations include eruption-wear and cementum annulus counting techniques (e.g., Marks & Erickson, 1966; Stoneberg & Jonkel, 1966). While beneficial to wildlife research, the applicability of cementum annulus counting is limited for paleontological populations both by the poor preservation potential of these fragile connective tissues and the technique's destructive nature. By contrast, evidence of tooth eruption and wear is preserved as long as the tooth element itself remains recognizable, and therefore is the approach to age-scoring favored here. The nondestructive aspect of eruption-wear approaches also allows more than one investigator the opportunity to study various dental aspects of a population, as well as to evaluate prior findings on mortality patterns in particular.

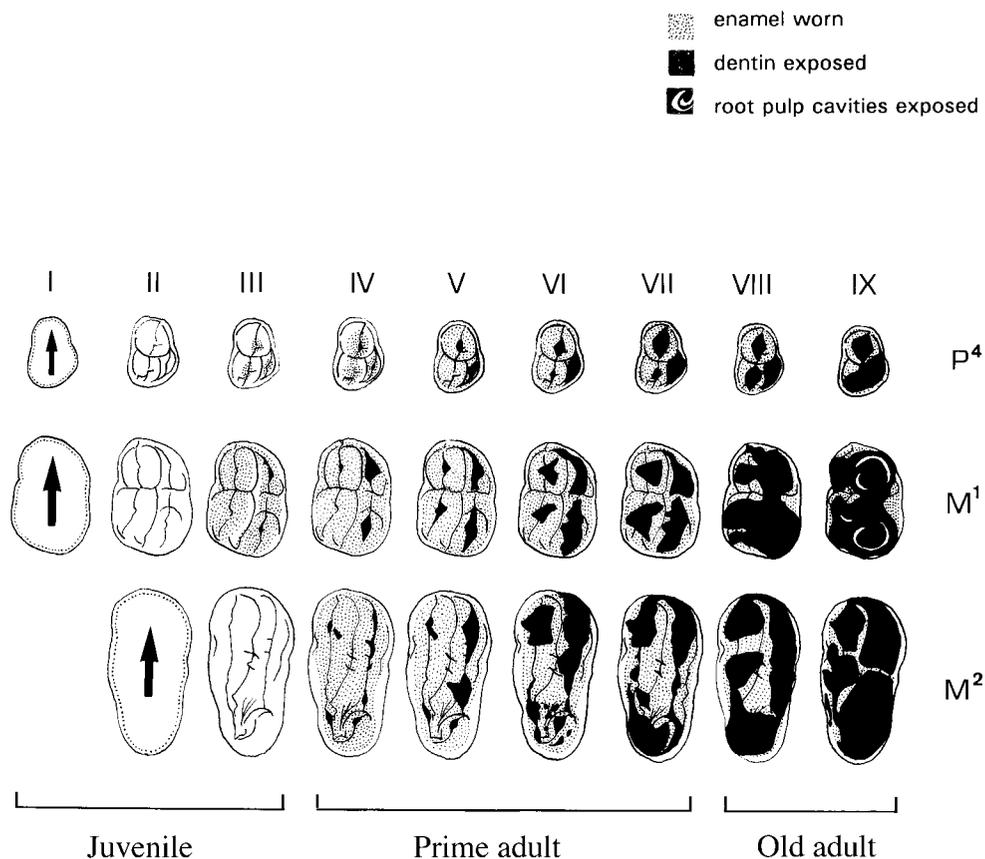


Figure 2. The tooth eruption wear stages for upper cheek teeth of cave and brown bears (genus *Ursus*), based on the P⁴, M¹, and M² (right side). The age stages are divided into nine cohorts, collapsible to three. The sequence begins with development of the deciduous tooth and/or the permanent counterpart (both in stage I, see text), followed by successive categories of occlusal wear; the arrow signifies that the permanent tooth crown is still emerging. The sequence ends (stage IX) with partial or complete destruction of tooth crown and exposure of the root pulp cavity, depending on the position of the element in the dental row. The M¹ represents the zone of greatest cumulative wear, and those for the P⁴ and the M² are adjusted to it. Note that the scheme does not attempt to estimate real age for any cohort, nor does it assume that the cohorts are of equal duration; neither assumption is necessary to the age structure comparisons. Drawings are of real, representative teeth and, for this reason, the wear patterns observed in other assemblages can not be expected to display perfect matches; the *total area* of enamel polish or dentin exposure is more important than the details of enamel loss.

animal's food processing apparatus is severely compromised or no longer functional (Stiner, 1990, 1994). The anterior molars may be best for age-scoring, because they emerge fairly early, they experience heaviest friction overall, and complete destruction of the tooth crown is possible with advanced age (Figures 2 and 3). Deciduous teeth are de-emphasized by this

scheme in favor of partly developed permanent teeth, because of the nominal structure of the deciduous elements and their short use-life in relation to the time at which cubs abandon the winter den to follow their mothers.

Because the bear tooth eruption-wear scheme is developed from real specimens, some variation between individuals,

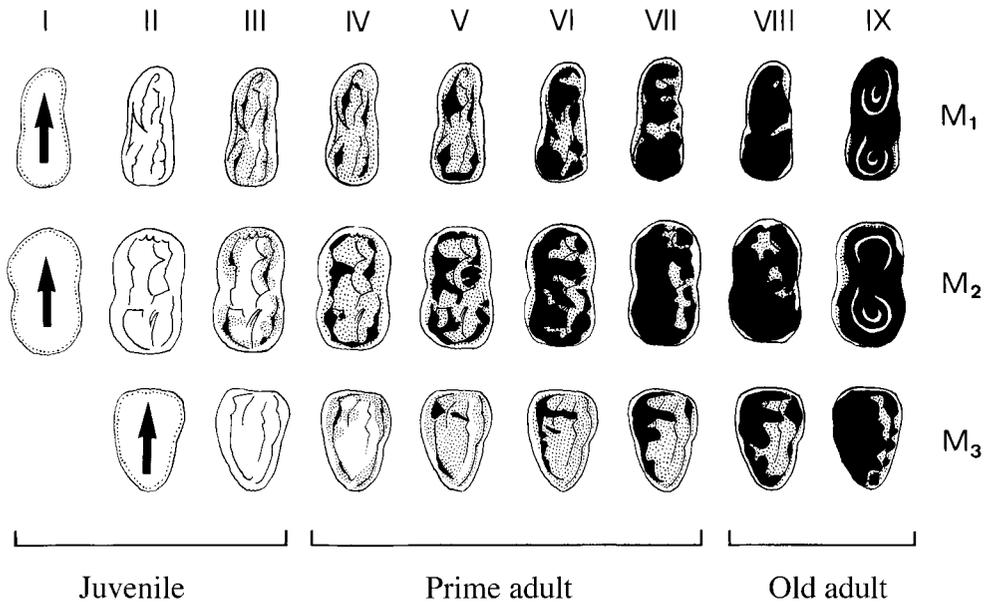


Figure 3. The tooth eruption wear stages for lower cheek teeth of cave and brown bears (genus *Ursus*), based on the M_1 , M_2 , and M_3 (left side). The age stages are divided into nine cohorts, collapsible to three. The sequence begins with development of the deciduous tooth and/or the permanent counterpart (both in stage I, see text), followed by successive categories of occlusal wear; the arrow signifies that the permanent tooth crown is still emerging. The sequence ends (stage IX) with partial or complete destruction of the tooth crown and exposure of the root pulp cavity, depending on the position of the element in the dental row. The M_1 and M_2 represent the zone of greatest cumulative wear, and wear for the M_3 is adjusted to them. Note that the scheme does not attempt to estimate real age for any cohort, nor does it assume that the cohorts are of equal duration; neither assumption is necessary to the age structure comparisons. Drawings are of real, representative teeth and, for this reason, the wear patterns observed in other assemblages can not be expected to display perfect matches; the *total area* of enamel polish or dentin exposure is more important than the details of enamel loss. The cusp morphology and wear patterns of the M_3 appear to be especially variable among individuals.

populations, and species is to be expected, both in the shapes of dentin patches exposed by occlusal wear and in the absolute correspondences between the onset of wear and completion of root development in young individuals (see also [Dittrich, 1960:133–135](#)). Inter-individual variation in the degree of tooth wear in mammals naturally increases with age (e.g., [Lowe, 1967](#); [Murie, 1951](#)). It also is likely that bear populations occupying distinct habitats experience somewhat different wear rates as a function of dietary fiber and grit (cf. [Andrews & Turner, 1992](#); [Baryshnikov, 1997](#); [Koby, 1940, 1953](#); [Kurtén, 1976:18ff](#); [Stiner *et al.*, 1998](#)). However, these are relatively minor

sources of ambiguity in this empirically derived nine-stage scheme and do not appear to be a problem for the simpler three-age scheme presented below.

Scoring system for nine age cohorts

Permanent cheek tooth eruption sequences in modern *Ursus* (following [Dittrich, 1960](#); [Kurtén, 1958](#); [Marks & Erickson, 1966](#)) are relatively uniform. Crown development begins with the upper and lower first molars (M_1), followed by fourth premolars (P_4), second molars (M_2), lower third molars (M_3), and finally the canines (C) (e.g., [Figure 4](#)). Eruption of lower third molar and canine crowns occurs during the second



Figure 4. Juvenile (male?, specimen 90-P-306) and adult (female, specimen 90-P-288) cave bear mandibles from Yarimburgaz Cave. Note the encrypted status and vertical position of the lower third molar during crown formation. At the same age, eruption of the second molar is nearly completed, but the canine crowns are only about 10% erupted. The posterior part of the tooth row “unfolds” as the growing jaw lengthens.

winter of life in modern bears; all of the permanent teeth with the exception of the canines will have pushed through the gums by end of first year, however. Permanent crown development normally is completed within the second year of life; root development is completed much later (e.g., [Poelker & Hartwell, 1973](#)).

Age stage I in [Figures 2](#) and [3](#) potentially combines counts for deciduous upper or lower canines with those for emerging but unworn permanent teeth. Brown bear cubs develop the full deciduous dentition only by the third month of life, and the first permanent molars (M1) emerge in the fifth month. Infant bears are especially altricial among carnivores ([Ewer, 1973:296, 332](#)), and their milk teeth are unimpressive ([Dittrich, 1960](#); [Kurtén, 1958](#)). Because the deciduous dentition of bears is less elaborate than those of canids or hyaenids, some qualifications to the definition of the juvenile versus adult cohorts in bears are required. Specifically, an analyst’s decision to include deciduous teeth in stage I must take into account the

fact that their presence in a living animal overlaps with erupting (countable) permanent tooth crowns for significant spans of time. Because deciduous teeth may straddle emerging permanent ones in a young bear, Stage I must include all permanent teeth from the germ stage to those with root lengths that are up to 50% complete, but only those deciduous teeth that display no wear to moderate wear. This procedure may slightly underestimate the total number of very young individuals for an assemblage, but it avoids the more serious problem of double-counting these individuals ([Stiner, 1994:322–324](#)).

Stage II is represented by a fully (or nearly) emerged permanent tooth crown, whose root development exceeds 50% of the normal length at maturity but whose occlusal surface lacks visible wear. Little wear normally occurs until after root formation is completed (95–100%). Thus, occlusal wear stages I–II include all phases of root development for permanent cheek teeth.

By stage III, root development is completed and some wear of the occlusal enamel is evident, but *little or no dentin* is exposed. A bear that dies during stage II or III would still be young, probably hibernating alongside its mother through a second or even a third winter. Stages IV through IX are based exclusively on the wear status of the occlusal surface. The reference assemblages used to develop the scheme reveal that the M_1 , M_2 , and M^1 can be worn down to the roots by stage IX in exceptionally long-lived individuals, often with the pulp cavities exposed. Age-scoring of the posterior molars (M_3 , M^2) therefore requires adjustments relative to the anterior molars to compensate for their “younger” appearance (see Figures 2 and 3).

Collapsing nine cohorts to three for comparisons to models in tripolar format

Phrased initially in terms of nine age stages, the eruption-wear diagrams in Figures 2 and 3 include guidelines for collapsing the data into three age stages—*juvenile* (I–III), *prime adult* (IV–VII), and *old adult* (VIII–IX). This is the most efficient way to examine the results in terms of modeled variation and the test implications outlined above. An additional advantage to this simpler scheme is its tolerance for small samples. As few as 12 individuals may be acceptable, although larger samples are preferred as a rule; this minimum threshold is considerably lower than that required for nine-cohort analysis, minimally 30 animals according to Lyman (1987).

The three simplified age stages—*juvenile*, *prime adult*, and *old adult*—effectively describe the essential differences among the age structure models in question. This is because the three age groups are divided according to major changes in physiology and behavior in the life histories of female mammals (see Stiner, 1990, 1994). The placements of the age divisions are important. The juvenile-prime adult juncture

compensates for the relatively precocious pattern of tooth development in carnivores relative to most herbivores by relegating slightly worn permanent teeth to the *juvenile* category. The transition to adulthood corresponds to the time at which females are first able to reproduce, regardless of whether they have learned enough to be competent parents. The prime-old adult age boundary is defined by a significant decline in adult female fertility, normally at about 67% of MPL. In modern brown bears this begins soon after 15 years of age, although cubs have been successfully whelped by female bears in the 22nd year of life (Craighead *et al.*, 1976:346–350). The onset of the reproductive decline in adult females therefore fits well with the 67%-of-MPL boundary established previously by Stiner (1990, 1994) for other mammals.

Figure 5(a) and (b) show how mortality data organized into the three age categories can be compared to a series of mortality models and their attendant variation (“pattern families”) in a tripolar format. The graph consists of three age axes [Figure 5(a)], each bisecting the triangle and ranging from 0 to 100%. By converting the frequencies of individuals in each age category to percentages of the total, the age structure based on a particular tooth element and population can be represented by a single point. Results for different tooth elements of the same population, or results based on one type of tooth for several populations, can be compared as multiple points on a single graph.

Figure 5(b) presents the interpretative standards—or models—for the mortality analysis. The areal distributions of five mortality pattern families are based on the real consequences of a host of mortality factors, including disease, accidents, malnutrition, and/or predation (from Stiner, 1990, 1994). Most important to this discussion are the two areas in the lower

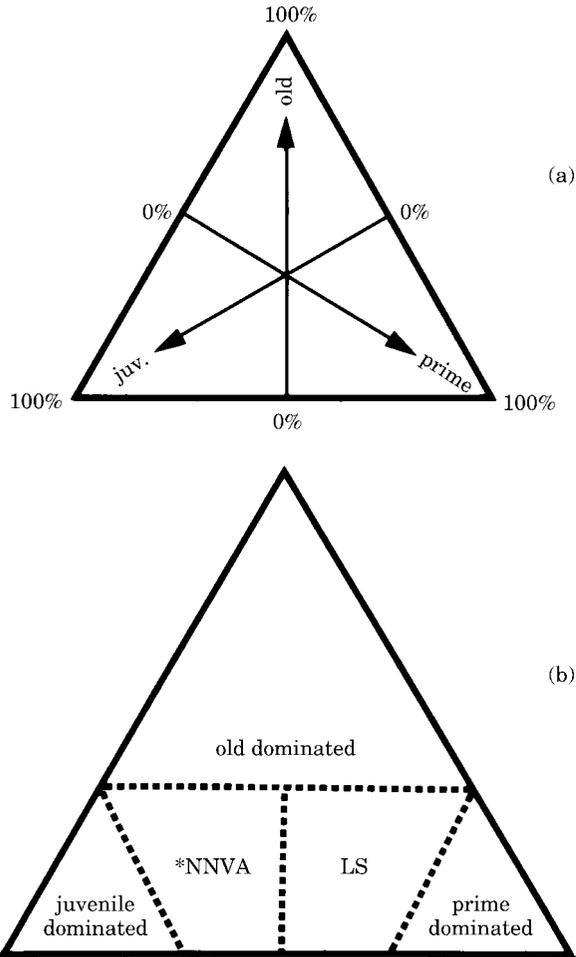


Figure 5. Guides for reading (a) the tripolar graphs and (b) the pattern map representing modeled variation associated with five distinct families of mortality patterns (from Stiner, 1990). Each area represents a mortality pattern family, incorporating both the average condition and normal variation surrounding it. Of greatest relevance to interpreting bear mortality patterns in cave sites are the normal non-violent attrition (NNVA) pattern family and the living structure (LS) pattern family. The area identified as NNVA (*) overlaps with mortality patterns generated in prey caught in open land conditions by cursorial predators (see Stiner, 1990, 1994), but this is not relevant to interpretation of hibernation-related mortality patterns in bears. *In situ* predation on den-bound bears should instead affect individuals randomly with respect to age and therefore result in a death pattern that resembles the living age structure (LS) of the hibernating population.

central zone of the graph, labeled normal non-violent attrition (NNVA) and living-structure (LS) patterns respectively (following Caughley, 1977 on mammals; for bears specifically, see Rogers, 1987; Bunnell & Tait, 1981; Eberhardt *et al.*, 1986; McCullough, 1981). Each corner of the graph represents a significant bias toward

the designated age group. As explained earlier, the prediction for bear assemblages representing hibernation deaths is the NNVA pattern type. The prediction for bear death assemblages representing primarily random predation *in situ* (e.g., by wolves, hyenas, or humans) is the LS pattern type.

Application to the Middle Pleistocene cave bear assemblage from Yarimburgaz Cave

The large bear death assemblage from Yarimburgaz Cave in northwestern Turkey (Arsebük *et al.*, 1990, 1991, n.d.; Arsebük & Özbaşaran, 1994; Howell & Arsebük, 1989, 1990; Özdoğan & Koyunlu, 1986; Stiner *et al.*, 1996) was used in part to develop this eruption-wear approach to mortality analysis, along with several smaller assemblages from Italian cave sites. Central to understanding the formation history of the Middle Pleistocene faunas in Yarimburgaz Cave is the question of why bears and Paleolithic artefacts occur in the same geological levels. Application to the Yarimburgaz sample illustrates the potential of the method for taphonomic research on other cases in which a temporal link between human and bear occupations is possible.

Yarimburgaz Cave consists of two internally connected chambers, the lower of which extends roughly 600 m into the limestone bedrock. Middle Pleistocene sediments (Blackwell *et al.*, 1990; Farrand, 1992) excavated within 70 m of the lower entrance are rich in both cave bear remains (Stiner *et al.*, 1996) and Paleolithic artefacts (Kuhn *et al.*, 1996). Bear bones constitute 93% of all macromammal specimens recovered from the Middle Pleistocene deposits; ungulate and non-ursid carnivore bones make up the remaining 4% and 3% respectively. Taphonomic investigations by Stiner, Arsebük & Howell (1996) indicate that the bone and artefact accumulations represent a palimpsest of multiple, discrete occupations of the cave by bears and hominids. Bear mortality data are among the important kinds of evidence pointing to this conclusion.

As many as 45 individual bears are represented in the bone assemblage, most of them a large variant of *Ursus* [*Spelearctos*] *deningeri*, accompanied by rare examples of a

small-bodied brown bear (*U. arctos*) (Stiner *et al.*, 1998). The skeletal remains are in a relatively advanced state of fossilization. The macroscopic features of the bones and teeth are very well preserved, as are traces of gnawing by various carnivores and, in other instances, small rodents (see Stiner *et al.*, 1996). Skeletal representation for the bears verges on anatomical completeness, also consistent with the hypothesis that the bear remains accumulated in the cave as the result of many hibernation-related death events.

The complete taphonomic evaluation of the Yarimburgaz case is in fact based on cross-referenced information on bone modification, species and body part representation, and mortality analysis, synthetic results on which are reported elsewhere (Stiner *et al.*, 1996). One arm of that investigation, focusing on bear mortality patterns, shows that the bear remains are primarily the result of non-violent mortality in hibernation dens (the NNVA model), not predator-caused mortality (the LS model). A result indicating predominantly non-violent mortality negates the possibility of temporal connections between humans' and bears' presence in the cave.

Table 1 presents age frequency data in nine-cohort format for the cave bears of Yarimburgaz, based on each of six different cheek tooth elements (P^4 , M^1 , M^2 , M_1 , M_2 , and M_3). All excavation units are combined in this comparison because the question is about the net consequences of multiple bear occupation and death events. A U-shaped, or bimodal, contour emerges in all of the histograms shown in Figure 6, with the possible exception of that for the P^4 . Two distinct peaks occur in cohorts III and VIII, whereas prime-aged adult bears are under-represented. To this point, the results obtained for the Yarimburgaz cave bears are broadly consistent with those obtained by Kurtén (1958) for cave bears from Odessa, Gargett (1996) for Pod Hradem in the

Table 1 Nine-cohort mortality data for Yarimburgaz cave bears based on six different cheek tooth elements

Tooth element	Number of age-scored teeth	MNI	Nine age cohorts:								
			I	II	III	IV	V	VI	VII	VIII	IX
P ⁴	37	19	7	7	9	5	5	5	0	1	0
M ¹	43	25	8	6	11	5	5	2	0	1	2
M ²	36	20	7	9	8	2	2	2	0	1	1
M ₁	65	35	5	6	20	13	13	7	5	1	4
M ₂	79	44	9	12	27	13	13	5	3	2	1
M ₃	62	39	7	13	15	7	7	4	4	3	2

Note: The number of age-scored teeth includes right and left elements. The minimum number of individual animals (MNI) is based on the most common side (right or left); it is not used for any of the calculations to follow but instead is provided as background information.

Czech Republic, Wiszniowska (1982) for Bacho Kiro in Bulgaria, and Andrews & Turner (1992) for cave bears from Westbury in Great Britain. Possible overlap of the observed patterns with other mortality models (especially LS) has not been refuted, however (see below).

A nine-cohort approach also reveals some interesting details about juvenile mortality in the cave bears. Stage III juveniles are especially prevalent. Two factors may contribute to this result. First, cubs younger than three months may not possess erupted teeth, and the partly formed deciduous tooth crowns developing below the gumline are not fortified by dentin and therefore may be more prone to destruction. A few very young cubs in Yarimburgaz Cave may have been completely ingested by predators, evidenced by a canid scat sample containing the bones of a hare and an infant bear (Stiner *et al.*, 1996). The low proportion of individual bears in cohort I could therefore be due partly to a low probability of preservation (see also Andrews & Turner, 1992:145–147). However, this explanation can not apply to cohort II, which also contains fewer individuals than cohort III. The cheek teeth of cohort II individuals would have been well-formed at the time of death and therefore as resistant to decomposition factors as the teeth representing cohort III.

The second factor contributing to the high proportion of individuals in cohort III may be heightened mortality for this late juvenile age stage. Indeed, the pattern for the Yarimburgaz cave bears is consistent with the situation among modern brown bears of North America (see, for example, Bunnell & Tait, 1981; Glenn *et al.*, 1976): the peak in cohort III likely represents the pivotal winter in which some juveniles found themselves alone for the first time since birth and many were unable to survive this critical transition period. The fact that adult female bears can spontaneously shed fertilized, unimplanted zygotes in years when the

foraging conditions prior to hibernation are poor may serve as a “bottleneck” beyond which only those cubs whose survival chances are very good make it to parturition. Modern bears are attentive mothers, fostering relatively high survivorship in cubs while under their care. Life may be far more difficult, by contrast, during the year in which young bears must begin to fend for themselves. Those abandoned early are at greatest risk.

Although the mortality histograms for the six tooth elements in Figure 6 could be said to differ from one another, a Kolmogorov–Smirnov test (Table 2) comparing the distributions shows that they yield fairly consistent results. Only three of the 15 pairwise age profile comparisons indicate differences at the 0.05 level of probability. The differences always involve upper-lower element pairings [Table 2(b)]; least agreement is found between the profiles for the M^2 and M_1 . The K-S test suggests—but does not prove—that all or most of the histograms are assignable to a single mortality pattern family.

The results presented thus far say nothing about how the findings relate to alternative mortality models—a question of what the observed patterns are not. In recognition of the variation that inevitably surrounds each idealized age structure model, the final step evaluates the extent to which a real case fits one model as opposed to all others. This procedure is very awkward in a two-dimensional format and often proves to be guesswork. It is relatively easy to obtain rigorous results by using the tripolar format outlined in Figure 5.

When the Yarimburgaz cave bear data are collapsed into the three age cohorts (Figure 7 and Table 3), it becomes clear that all of the age structures indicated by the six cheek teeth fulfill the NNVA prediction. The nine-cohort histograms vary in their contours (Figure 6), but not enough to warrant their classification as substantially different types

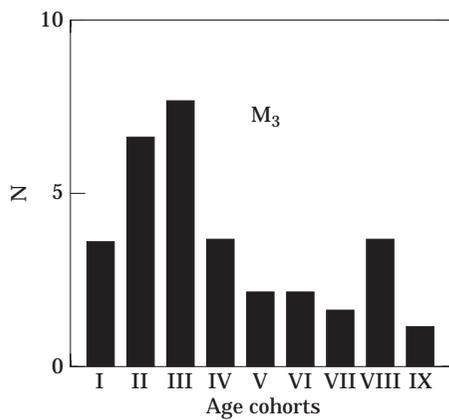
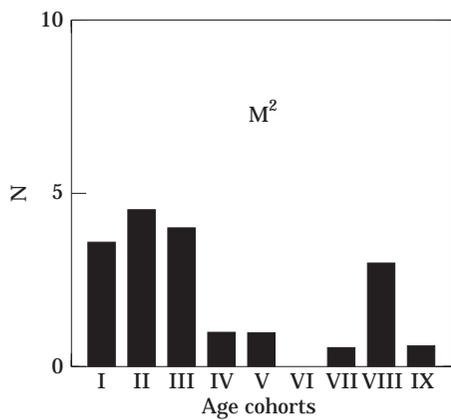
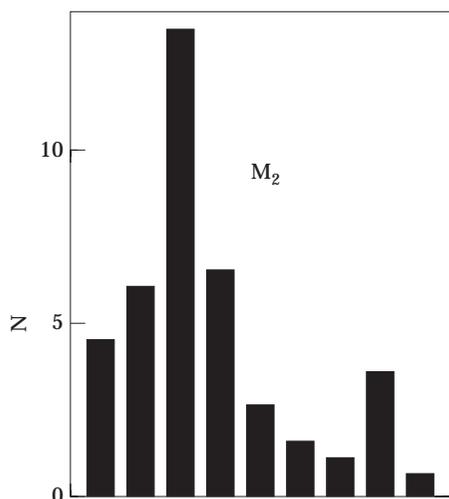
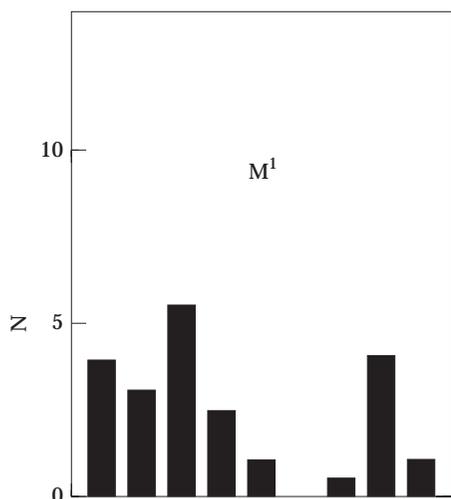
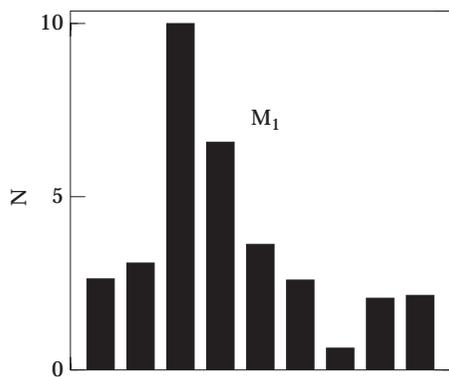
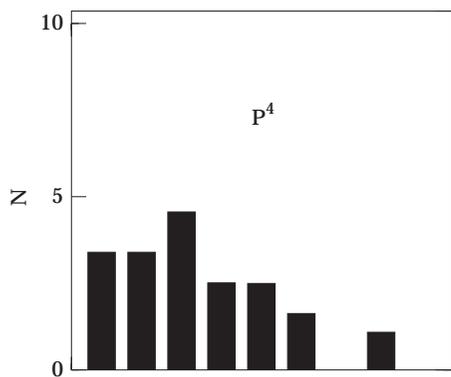


Table 2 Kolmogorov-Smirnov two sample test results of a comparison of mortality profiles for the Yarimburgaz cave bears, based on six different cheek tooth elements

(a) K-S values:

	M ₁	M ₂	M ₃	M ¹	M ²	P ⁴
M ₁	0.0					
M ₂	0.131	0.0				
M ₃	0.163	0.107	0.0			
M ¹	0.238	0.170	0.112	0.0		
M ²	0.366	0.290	0.208	0.151	0.0	
P ⁴	0.306	0.233	0.175	0.225	0.194	0.0

(b) two-sided probability values:

	M ₁	M ₂	M ₃	M ¹	M ²	P ⁴
M ₁	1.000					
M ₂	0.581	1.000				
M ₃	0.380	0.835	1.000			
M ¹	0.106	0.393	0.877	1.000		
M ²	0.003 ¹	0.028*	0.261	0.722	1.000	
P ⁴	0.021 ¹	0.112	0.435	0.228	0.452	1.000

*Differences that are significant at the 0.05 level of probability.

of mortality pattern (Figure 7). The upper and lower molars of the bears form separate subgroups on the tripolar graph, but all yield essentially the same answer.

The NNVA mortality pattern of the Yarimburgaz cave bears is consistent with hibernation-related deaths arising primarily from starvation and disease. This mortality pattern, which affects mostly young and old individuals, differs significantly from randomly-selected age groups normally found in hibernation dens. The NNVA mortality pattern of the Yarimburgaz cave bears therefore can not be explained as resulting primarily from surprise attacks by hominids, wolves or hyenas. What damage occurs on

the bear remains is attributable to non-ursid large carnivores (wolves and/or hyenas) and occasional cannibalism by other bears (Stiner *et al.*, 1996; see also Gargett, 1996 on Pod Hradem). Hunted bears cannot be distinguished from scavenged ones on the basis of bone damage, but the mortality evidence strongly argues for deaths primarily from starvation and other non-violent attritional factors, and that the remains of the bears were subsequently scavenged by predators. While some bear bones exhibit traces of gnawing, no cut marks were found. It seems that humans were not among the scavengers that utilized bear carcasses in Yarimburgaz Cave.

Figure 6. Age structure histograms for the Yarimburgaz bear death population based on six different cheek tooth elements and nine age stages. All of the histograms display U-shaped, bimodal contours in this two-dimensional format due to a relative paucity of prime-aged adults, with the possible exception of that for the P⁴. The profiles exhibit subtle variation among tooth elements. Juveniles in cohort III are especially prevalent in most profiles, possibly representing deaths following/during the first winter of independence. N represents the average number of individual bears, calculated by summing right and left sides of a given tooth element and dividing the sum by two.

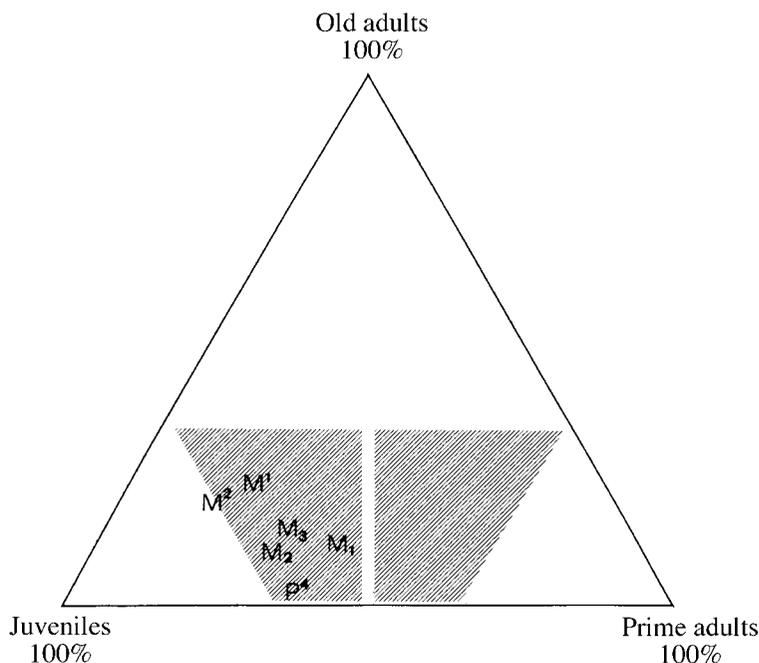


Figure 7. Three-age results for six different cheek teeth of Yarimburgaz bears graphed in tripolar format. The distribution shows that the mortality data for the Yarimburgaz cave bears fall within the NNVA pattern family; each of the six cheek tooth elements indicates a classically attritional age structure for the death population, consistent with the expectation of non-violent mortality in hibernation dens. The possibility that the mortality pattern of the Yarimburgaz cave bears resembles the living structure (LS pattern family) of the hibernating population is falsified. (This figure is reprinted with permission from "Cave bears and Paleolithic artefacts in Yarimburgaz Cave, Turkey: dissecting a palimpsest", by M. C. Stiner, G. Arsebük, and F. C. Howell, *Geoarchaeology* copyrighted 1996, Academic Press.)

Table 3 Mortality data for Yarimburgaz bears, using three age cohorts

Tooth element	Number of age-scored teeth	Percentages of total:		
		Juvenile	Prime adult	Old adult
P ⁴	37	62%	35%	3%
M ¹	43	58	19	23
M ²	36	67	14	19
M ₁	65	48	40	12
M ₂	79	61	29	10
M ₃	62	56	29	14

Discussion

Although the more obvious benefit of mortality data on Pleistocene bears may be in the area of bear paleoecology, the mortality patterns of bears in caves are also important to paleoanthropological research. A review

of how modern bears live renders bear-artefact associations in Pleistocene caves remarkable in relation to modern human-bear interactions. The fact that any cave could have been frequented repeatedly by bears, Paleolithic hominids or other

carnivores suggests that human use of these places was relatively ephemeral and/or that occupations were separated by long intervals. Hibernation deaths in bears are seasonal phenomena and might occur when human occupation of the same place was least likely. However, any sign of recent disruption at a shelter can be enough to dissuade a den-seeking bear—their great vulnerability during dormancy requires that the hibernation lair be kept secret. The common presence of bear skeletal remains and stone artefacts in Paleolithic caves of Eurasia therefore suggests extended windows of safe use for bears. It is likely under these circumstances that the occupations by humans and bears were widely scattered in time, on the order of decades or longer, and that claims of the shelter by any prospective occupant hinged primarily upon a low risk of interference or disturbance.

Mortality patterns add a unique and valuable dimension to research on the circumstances of bear–artefact associations in Paleolithic shelter deposits. The age structure of Middle Pleistocene cave bears from Yarimburgaz Cave falls squarely into the NNVA pattern family and is exactly what one would expect to result from primarily non-violent attrition in a hibernation den context. Mortality data therefore are among the kinds of evidence that negate the possibility of any direct causal (temporal) link between bear and hominid occupations of Yarimburgaz Cave, arguing instead that the bears used the cave privately as a hibernation lair over many generations. The boundaries dividing the three age stages provide a relatively coarse description of age structure, yet they prove effective for taphonomic investigations of carnivore presence in Paleolithic caves (see also [Stiner, 1994](#)).

It is, however, the combination of multiple independent sources of information that constitutes a compelling argument for hibernation deaths as the main or sole cause

of the bear bone accumulations in the cave. The mortality data are simply one highly desirable line of evidence. Of course the value of mortality analysis is contingent on how it is applied. The method presented here fosters replicability of results and their interpretation across studies by pushing analysis beyond simply choosing an explanation to testing it. The method has the power to isolate contrasting outcomes, because the age divisions used are closely allied to major transitions in the life course, and the reference models are developed from independent empirical and theoretical sources. Needless disagreements among researchers have occurred in the recent zooarchaeological literature simply for the lack of independent standards for constructing, classifying, and interpreting age structure profiles.

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