

Natural-trap ursid mortality and the Kurtén Response

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Abstract

Ursid mortality data have long been used to evaluate associations between cave-bear remains (*Ursus deningeri* and *U. spelaeus*) and hominin (*Homo* sp.) remains. Typically, such ursid assemblages produce mortality patterns that indicate that juvenile and old bears died during hibernation, a pattern that is used to suggest that humans and bears occupied the same caves at different times. However, a different kind of mortality pattern can also be used to suggest human influence on cave bears, particularly under circumstances when bears and humans compete for habitat. In particular, data from Lawson Cave and Jerry Long Cave, Missouri indicate that young-adult North American black bears (*Ursus americanus*) are prone to capture in natural-trap caves. Similar faunal data from Sima de los Huesos in Spain, where cave-bear and hominin remains are found in the same deposit, might also suggest that the bears died from falling into a natural trap. It is concluded that mortality analysis of ursid remains from caves is a useful tool with which to evaluate accumulation histories of cave deposits and relations between humans, artifacts, and cave-bear remains. In particular, ursid mortality data are relevant to the Kurtén Response, a hypothesis reiterated in the recent literature that implicates human encroachment on ursid habitat (e.g., cave den sites) as a potential cause in cave-bear extinction. © 2006 Elsevier Ltd. All rights reserved.

Keywords: Black bear; Extinction; Cave fauna; Cave bear; Missouri caves

Introduction

Archaeologists have long taken an interest in interaction between humans (*Homo* sp.) and extinct European cave bears (*Ursus deningeri* and *U. spelaeus*) because the skeletal remains of these bears regularly occur in Late Pleistocene deposits that also contain cultural material (see Kurtén, 1976; Stiner, 1998). Of particular interest is the role (or lack thereof) that hominins played in the extinction of cave bears. Recently, it has been proposed by Grayson and Delpech (2001, 2003) that cave bears potentially became extinct because they were out-competed by an expanding human population for crucial habitat, such as cave den sites, during the Late Pleistocene. Grayson and Delpech (2001, 2003) call this the Kurtén Response after renowned paleontologist Bjorn Kurtén who maintained a career-long interest in cave-bear faunas.

The focus of this paper is mortality analysis for two reasons; first, such data have proved useful in helping

archaeologists understand the taphonomic histories of cave-bear faunas, particularly regarding how ursid remains came to be deposited in caves (e.g., Webb, 1988; Gargett, 1996; Stiner et al., 1996; Garcia et al., 1997). Second, because of this utility, it is argued that mortality data might provide a useful test implication regarding the hypothesized Kurtén Response. I argue that prime-adult-dominated ursid mortality in natural traps can be used to understand competition for habitat between humans and bears. Ecological and behavioral characteristics of young-adult ursids explain why members of this age group are more likely than other bears to seek food (e.g., carrion) in dangerous locations like natural traps. Moreover, in periods during which humans encroach upon available habitat (e.g., historic-period North America), there are reasons to expect that young-adult bears are even more susceptible to such deaths. Perhaps the Late Pleistocene in Europe was a similar setting in that hominins and cave bears appear to have used many of the same caves and because the presence of hominins in significant numbers, as fellow omnivores, would have encroached on cave-bear habitat in

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general. As a result, mortality characteristics of ursids are directly relevant to testing the Kurtén Response hypothesis (*sensu* Grayson and Delpech, 2003). This paper focuses, thus, on three things—a cursory introduction to ursid food habits and mortality, brief but important taphonomic histories of two North American black-bear faunas, and how characteristics of those black-bear faunas are important in discussion of the Kurtén Response.

Cave bears and shapes of mortality patterns

For many years it was argued that humans hunted cave bears as they hibernated in caves during the winter (see summaries in Kurtén, 1976 and Stiner, 1998). However, mortality data indicate that hunting of hibernating cave bears was rare. Bears of all ages hibernate, would have been vulnerable to predation during hibernation, and would have been hunted when encountered. As a result, mortality patterns should reflect encounter probability determined by ursid population structure. Thus, assemblages representing this kind of predation are predicted to produce age structures containing individuals of all age groups in roughly the proportions found in living populations (L-shaped mortality¹)—with high abundance of juveniles, medium abundance of young, healthy adults, and low abundance of old adults (e.g., Lyman, 1987; Stiner, 1998) (Fig. 1). However, many cave-bear faunas produce mortality patterns that are not L-shaped but instead are proportionally abundant in remains of juvenile and old-adult bears (U-shaped mortality). Individuals in these age classes would have been susceptible to natural deaths during hibernation (Webb, 1988; Gargett, 1996; Stiner, 1998). Thus, it appears unlikely that hominins hunted cave bears in most settings, but rather that bears hibernated and died natural deaths in many cave faunas.

Although zooarchaeologists and paleontologists interested in cave-bear mortality have focused on U- versus L-shaped mortality patterns, another type of pattern, prime-dominated mortality, is of potential use in studying cave-bear taphonomy. For example, young prime-adult bears are vulnerable to entrapment in natural-trap caves and are highly susceptible to death in such settings (Wolverton, 2001). Natural traps are caves with vertical entrances that allow animals to enter, but exit is prohibited via the same entrance usually because of steep or inverted entrance walls. Often animals die from falling into such caves or of starvation after surviving a fall, and as a result carrion accumulates (e.g., Oliver, 1989). Spatial association between cave-bear and human remains might be the result of several factors because cave structures change through time, such as occurs with the collapsing of vertical or horizontal entrances and the opening of new ones, which

¹ “U-shaped” and “L-shaped” are descriptions of the shapes of age-structure histograms; U-shaped histograms have high representation of juveniles and old adults, and L-shaped histograms have high representation of juveniles relative to prime and old adults. Zooarchaeologists and paleontologists now use these terms to denote kinds of age structures: U-shaped patterns reflect attritional deaths of vulnerable juveniles and old adults, and L-shaped patterns suggest non-selective mortality within a living population.

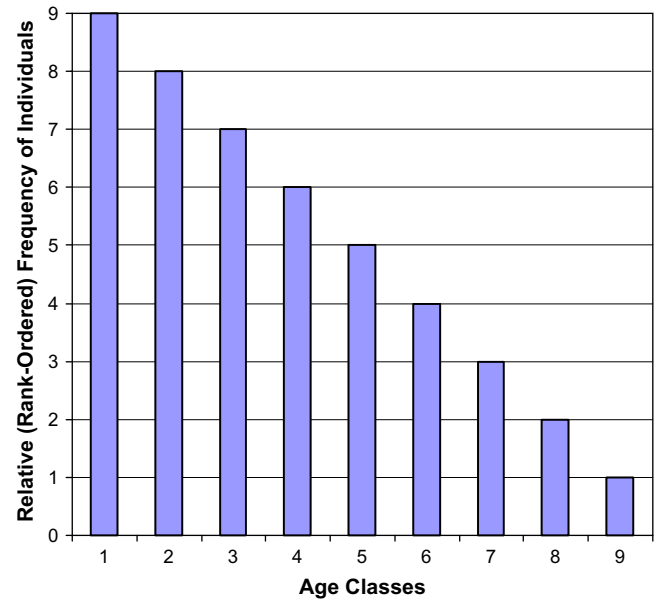


Fig. 1. Theoretical rank-order living structure model proposed by Lyman (1987, Fig. 3) presented here using nine age classes.

might expose faunal assemblages to a diversity of taphonomic agents over time. In particular, European caves that have or had vertical and horizontal entrances might have served as burial sites or shelter to humans and acted as traps to cave bears (Andrews and Fernandez-Jalvo, 1997). Consideration of North American black-bear (*Ursus americanus*) remains from natural traps suggests that such assemblages are identifiable using mortality data in that young prime-aged adults dominate them (Wolverton, 2001). This mortality pattern is different than L-shaped and U-shaped mortality patterns and occurs for a distinct reason—young adults are particularly susceptible to accidental deaths.

Research on modern North American bears indicates that young-adult individuals are more susceptible to poor health and accidental death than other bears (e.g., Poelker and Hartwell, 1973; Garshelis and Hellgren, 1994). For example, McLellan et al. (1999) report that young male grizzly bears (*Ursus arctos*) in the Pacific Northwest of North America have high mortality rates compared to mature adults that have established home ranges. Young-adult black bears disperse in order to establish new territories, and this is a particularly vulnerable period in their lives. For example, Rogers' (1987) research on a black-bear population from northern Minnesota demonstrates that young adults, especially males, experience relatively low survivorship compared to juveniles and prime adults (Fig. 2). In fact, it is not until individuals approach old age that survivorship is lower than during subadult dispersal at three to four years of age. Another study by Dobey et al. (2005) also highlights relatively low survivorship in young adults during dispersal from their natal home range to establish new territories (Fig. 2).

Dispersal is a stressful event in the lives of bears, a point that is made clear in a study on black-bear health in Washington State (Poelker and Hartwell, 1973). Subadult bears experience poor health relative to bears in other age classes

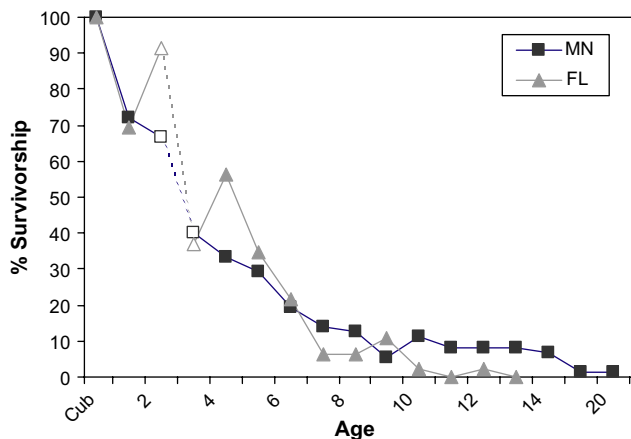


Fig. 2. Percent-survivorship profile for black bears from Minnesota ($n = 125$) and Florida ($n = 203$) (data from Dobey et al., 2005 and Rogers, 1987). The open squares and triangles connected by dashed lines represent high mortality rates during dispersal in both samples. Increases through time reflect infrequent immigration into study areas by bears.

(Table 1). Health, or condition, of bears was measured in terms of disease and parasite loads and hematology; of the twenty-five bears studied, only one subadult was described as healthy. Limiting factors on establishing new home ranges include access to food and mates, both of which bears must compete for during and after dispersal (Powell et al., 1997). It follows that young-adult bears, more desperate in the search for both resources, are more likely to enter into unknown habitat, dangerous locations, and indirect and direct conflict with other predators (including other bears and humans) during dispersal. Much of this risk is wrapped up in the search for food.

During the Late Pleistocene, hominins entered and became more prevalent in Europe; their growing presence through time likely influenced cave bears. Among these bears, it was young adults dispersing from a lifestyle dependent on their mothers that would have been susceptible to direct and indirect competition with hominins. If competition for habitat, caves, or even food was severe enough, then young-adult bears should have been progressively more susceptible to accidental deaths (including via natural traps) through time.

How herbivorous are modern bears?

It might be argued that black bears cannot serve as an analog for cave-bear behavior. The argument presented here is that cave bears, particularly young adults, would have

Table 1
Condition of black bears in western Washington (Poelker and Hartwell, 1973)

Health status	Females ($n = 12$)	Males ($n = 13$)	Total ($n = 25$)
Poor to fair condition	*Y = 1	Y = 1	Y = 2
	SA = 2	SA = 3	SA = 5
	A = 2	A = 1	A = 3
Good to excellent condition	Y = 1 (anestrus)	Y = 1	Y = 2
	SA = 1 (estrus)	SA = 0	SA = 1
	A = 5 (2 estrus)	A = 7	A = 12

*Y = yearling, SA = subadult, A = adult.

been attracted to carrion because modern members of *Ursus americanus* are attracted to carrion. Isotope studies indicate that cave bears (*U. deningeri* and *U. spelaeus*) were primarily vegetarians. For example, Bocherens et al. (1994) provide an analysis that compares cave-bear diet to those of other bears and to herbivores in general. There is fine-scale dietary diversity among bears (excluding the polar bear *U. maritimus*). All omnivorous members of *Ursus* are less vegetarian than pure herbivores, but cave bears appear to have been the most vegetarian of all. Bocherens et al. (1994) demonstrate, however, that cave bears were pure herbivores. However, there is diversity in vegetarianism among modern bears. Of the modern members of *Ursus*, the North American black bear is useful in comparison to cave bears because it is relatively herbivorous. For example, among mid-twentieth-century Yellowstone National Park black bears, one study estimated that over 80% of fecal matter was plant material (Schullery, 1992), and these were bears that had access to garbage and handouts from tourists. Vegetarian diet of Yellowstone black bears ranges from berries, to roots and tubers, even to cambium from interior bark layers of trees. Boileau et al. (1994) provide similar data on seasonal use of food resources by black bears in Quebec; vertebrate sources, in their study, comprised only nine percent of bear diet. Black bears, like cave bears, are primarily vegetarian.

The issue is not whether or not cave bears were vegetarian; the issue is whether or not cave bears, like black bears, would have eaten meat when they encountered it. Their carnivorous heritage suggests that they would have. In fact, “though vegetation comprises the bulk of the [black] bear’s diet, there are times when meat has considerable significance, and it is always of interest” (Schullery, 1992:14, emphasis added). However, the black bear is not as carnivorous as some other members of *Ursus*: “the black bear’s attitude toward meat, especially in great quantities, is more casual than the grizzly’s” (Schullery, 1992:15). For example, black bears do not cache meat like grizzlies (*U. arctos*), but they do travel long distances to acquire it (Brown, 1993).

Following these age-dependent health and behavioral characteristics, relatively young black bears are more likely to have entered vertical-shaft caves to scavenge carcasses because they would have been establishing home ranges relative to availability of food, availability of mates, and competition with other bears (e.g., Powell et al., 1997; for more information on ursid home ranges and feeding strategies, see Klenner, 1987; Klenner and Kroeker, 1990; Beecham and Rohlman, 1994; Craighead et al., 1995). Further, if habitat is limited through interspecific competition with humans, young adults are even more vulnerable because dispersal becomes more difficult. It is this relationship between ursid mortality, habitat availability, and interspecific competition that is potentially relevant to cave-bear extinction during a period (the Late Pleistocene) when hominin presence in Europe gradually increased.

In short, young prime adults are under more stress than other bears and as a result are more likely to attempt feeding on carrion in dangerous locations (e.g., carcasses in natural

traps). This relationship for black bears has been studied using data from Lawson Cave in a previous study (Wolverson, 2001); here, the argument that ursid mortality data offer a useful tool to evaluate the relationship between cave bears and hominins in Europe is considered with a more robust North American black-bear sample produced by supplementing the Lawson Cave data with those from Jerry Long Cave—another vertical-shaft, natural trap from eastern Missouri.

A historic-period bear mortality analog

Two North American black-bear faunas are used to develop an analog relevant to testing the Kurtén Response hypothesis; both faunas are from natural-trap caves. Lawson Cave is a vertical-shaft cave located in central Missouri (Fig. 3). The cave was excavated during the 1950s by faculty and students of the University of Missouri zoology department. The deposit was completely excavated and screened through $\frac{1}{4}$ inch mesh, and all excavated faunal material was kept for analysis (Table 2). In profile, the cave is roughly bottle shaped; the natural trap is 11.5 meters deep, with an entrance that is 1.78 by 0.79 meters. Although a collapsed horizontal entrance adjoins the vertical shaft, it is 4.5 meters above the inverted walls of the trap; thus, even when it was open, it did not serve as an exit from the trap chamber. Remains of 10 individuals were recovered from the cave (Table 2), and the capture of primarily young-adult bears was not a result of sampling error (Wolverson, 2001). Ursid remains from the cave have been radiocarbon dated to the historic period (Wolverson, 1996, 2001; Wolverson and Lyman, 1998).

The remains of 12 black bears were recovered from Jerry Long Cave in southeastern Missouri (Table 3; Fig. 3). The

Table 2
Faunal remains from Lawson Cave (Wolverson, 2001)

Species	NISP
Black bear, <i>Ursus americanus</i>	445
Cottontail, <i>Sylvilagus floridanus</i>	238
Domestic pig, <i>Sus scrofa</i>	170
Woodchuck, <i>Marmota monax</i>	66
Dog or coyote, <i>Canis</i> sp.	66
Opossum, <i>Didelphis marsupialis</i>	42
Wood rat, <i>Neotoma</i> sp.	33
Vole, <i>Microtus</i> sp.	19
Deer mouse, <i>Peromyscus</i> sp.	18
Striped skunk, <i>Mephitis mephitis</i>	12
Squirrel, <i>Sciurus</i> sp.	7
White-tailed deer, <i>Odocoileus virginianus</i>	5
Eastern mole, <i>Scalopus aquaticus</i>	3
Raccoon, <i>Procyon lotor</i>	1
Beaver, <i>Castor canadensis</i>	1
Plains pocket gopher, <i>Geomys bursarius</i>	1

cave was carefully excavated and sieved through $\frac{1}{4}$ inch mesh; all recovered faunal specimens were kept for analysis. Parmalee and Jacobson (1959) describe a vertical fissure at the rear of the cave that is roughly 15 meters deep, which functioned as a natural trap. There are no Late Pleistocene taxa in the sample and historic debris was intermixed with the cave's faunal material. Parmalee and Jacobson (1959) conjecture that the remains were likely deposited during a few-hundred-year period just prior to the present. The taxa represented in the fauna tend to be those occurring today in deciduous-forest habitat surrounding the cave (Table 3).

The environmental setting in which ursid remains were deposited at Jerry Long Cave and Lawson Cave is important in

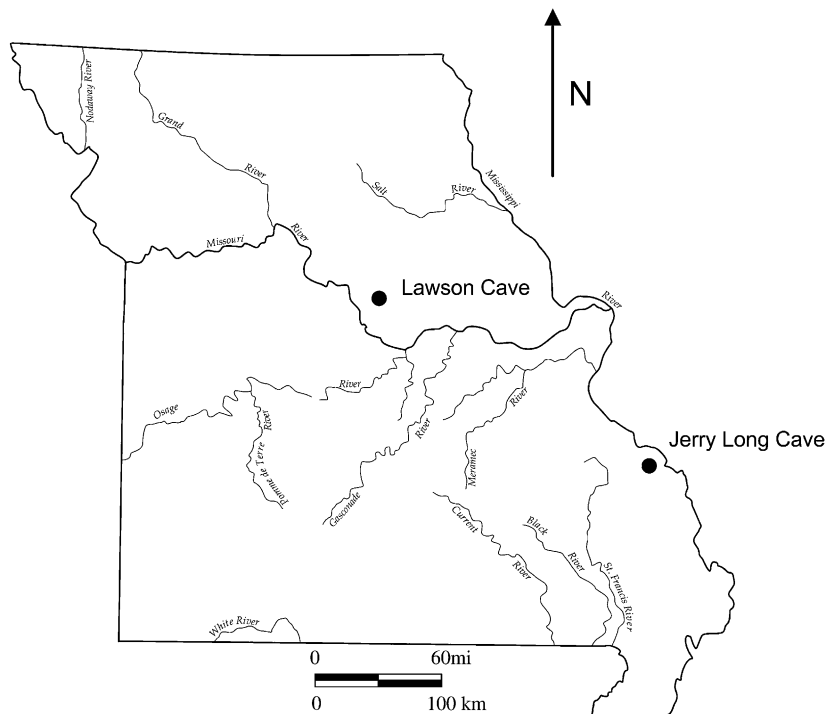


Fig. 3. Map of Missouri showing the locations of Lawson Cave and Jerry Long Cave.

Table 3
Faunal remains from Jerry Long Cave identified by Parmalee and Jacobson (1959)

Species	NISP
Eastern wood rat, <i>Neotoma floridana</i>	437
Woodchuck, <i>Marmota monax</i>	388
Black bear, <i>Ursus americanus</i>	222
Cottontail, <i>Sylvilagus floridanus</i>	93
Fox squirrel, <i>Sciurus niger</i>	66
Spotted skunk, <i>Spilogale</i> sp.	39
Striped skunk, <i>Mephitis mephitis</i>	37
Bobcat, <i>Lynx rufus</i>	33
Raccoon, <i>Procyon lotor</i>	38
Opossum, <i>Didelphis marsupialis</i>	11
Modern human, <i>Homo sapiens</i> ^a	9
Vole, <i>Microtus</i> sp.	9
Beaver, <i>Castor canadensis</i>	5
Big brown bat, <i>Eptesicus fuscus</i>	4
Eastern mole, <i>Scalopus aquaticus</i>	3
White-tailed deer, <i>Odocoileus virginianus</i>	3
Brown bat, <i>Myotis</i> sp.	2
Gray fox, <i>Urocyon cinereoargenteus</i>	2
Red fox, <i>Vulpes vulpes</i>	2
Deer mouse, <i>Peromyscus</i> sp.	2
Mountain lion, <i>Felis concolor</i>	2
Mink, <i>Mustela vison</i>	1
Bog lemming, <i>Synaptomys cooperi</i>	1
Turkey vulture, <i>Cathartes aura</i>	291
Screech owl, <i>Otus asio</i>	2
Turkey, <i>Meleagris gallopavo</i>	1
Prairie chicken, <i>Tympanuchus cupido</i>	1

^a Cranial fragments only, origin unknown (Parmalee and Jacobson, 1959).

developing an analog with which to evaluate the Kurtén Response. The historic period in Missouri was one of ever-increasing human population density, expanding use of arable land for farming, and, as a result, intensifying competition between black bears and humans for habitat. Black bears were extirpated in Missouri by roughly AD 1900. The observed distinctive mortality pattern of ursid natural entrapment combined with the historical context of habitat competition between black bears and humans is used here as an analog with which to derive a test implication for the Kurtén Response hypothesis. If European cave bears were being out-competed for habitat during the Late Pleistocene—like black bears in Late Holocene Missouri—then higher frequencies of young ursids should have been under nutritional stress and should have been susceptible to death by natural entrapment.

Use of such an analog to study prehistoric ursid population dynamics requires, at a minimum, three assumptions. First, the sample of ursid remains with which the zooarchaeologist works must be considered indicative of prehistoric life and death age structures (Stiner, 1990, 1994, 1998). This is a sampling problem inherent in most kinds of archaeological inquiry; the assumption is warranted if the analyst can provide a statement on the condition of the faunal sample in which various taphonomic agents are disconfirmed as important influences on the sample's accumulation history (see below). However, at some level, the analyst must assume that ursid mortality data reflect what Clark and Kietzke (1967:117

[Fig. 53], cited in Lyman, 1994a [Fig. 2.2]; see also Klein and Cruz-Urbe, 1984) refer to as the “death assemblage.” Second, use of the analog requires the assumption that young-adult ursids responded to habitat encroachment by humans during the Late Pleistocene in much the same way that modern ursids respond to habitat limitations imposed by modern humans. Such an assumption is warranted in that cave-bear remains are assigned to the same genus—*Ursus*—as many extant ursids, including the North American black bear. The appropriateness of Linnaean taxonomy in reference to fossil species is not considered here; rather, at issue is whether or not cave bears were “bear like” compared to modern ursids (see discussion above). A solid argument can be made that cave bears were quite “bear like” (e.g., Kurtén, 1976; Noonan et al., 2005), but that argument and use of the proposed analog, nonetheless, is assumptive. Third, and along similar lines, the analog requires the assumption that at a minimum most bears, and those under nutritional stress in particular, are attracted to carrion (see discussion above). Such is indeed the case among modern members of *Ursus* (Schullery, 1992; Beecham and Rohlman, 1994). Given that these assumptions are warranted, modern ursid mortality data from two faunas introduced below can be used to derive a new test implication concerning the Kurtén Response and cave bears in Europe.

Methods

The age-scoring technique

The ursid age-scoring technique designed by Stiner (1998) is used to determine the ages at death of bears trapped in Lawson Cave and Jerry Long Cave. Use of tooth wear to determine ontogenic age of mammals is controversial, but most analysts agree that wear is useful as an ordinal-scale measure of age and such techniques have been applied to ursids elsewhere (Kurtén, 1958; Rausch, 1961; Garcia et al., 1997; Stiner, 1998). Tooth-wear analysis has the added advantage of being non-destructive. The sample from Jerry Long Cave contains 41 upper and lower ursid molars; the sample from Lawson Cave contains 59 upper and lower molars (Table 4). The number of identified specimens (NISP) is used here to measure tooth frequency; all teeth are either complete isolated specimens or are from intact and partially intact mandibles and maxillae, thus the minimum number of elements (MNE) equals NISP. Left and right teeth are pooled, and the number of bears represented in each age class is potentially inflated as a result. However, as should be expected in complete excavation of natural traps, there is a fairly balanced ratio between right and left teeth in both samples (Jerry Long Cave: 18 left molars, 23 right molars; Lawson Cave: 31 left molars, 28 right molars). Consideration of left and right molars separately does not obscure the pattern that teeth from young, prime-aged individuals are frequently represented (e.g., Wolverson, 2001) (Fig. 4; Table 4).

A problem with using ursid tooth wear to determine ontogenic age at death is that different teeth wear at varied rates during individuals' lifetimes (Andrews and Turner, 1992).

Table 4
Frequencies (MNE) of each tooth type assigned to wear stages and life-history phases

Wear Stage	M ¹	M ²	M ₁	M ₂	M ₃
Jerry Long Cave					
1 juvenile	—	—	—	—	—
2 juvenile	1	1	1	1	1
3 juvenile	1	1	2	1	2
4 prime	2	2	3	2	3
5 prime	2	2	2	—	1
6 prime	2	2	1	2	1
7 prime	1	1	—	—	—
8 old	—	—	—	—	—
9 old	—	—	—	—	—
Lawson Cave					
1 juvenile	—	—	—	—	—
2 juvenile	—	—	—	—	—
3 juvenile	2	1	1	—	—
4 prime	1	4	2	2	1
5 prime	6	5	4	4	3
6 prime	1	—	2	1	2
7 prime	2	1	2	2	2
8 old	1	1	1	2	1
9 old	—	—	—	1	1

There are two strengths to using *Stiner's* (1998) wear schedule related to this problem. First, her wear schedule is ordinal scale; however, there are points in the schedule that signal particular life-history events. For example, dental eruption of permanent molars occurs during the juvenile stage, and wear begins in the adult stage. Although the precise ages of individuals based on these characteristics cannot be directly determined, it is clear that a fully erupted, unworn (or very lightly worn) upper or lower molar is not from a juvenile individual and not from an old adult. In fact, a tooth with these characteristics is likely from a young adult because the longer an individual possesses a full complement of adult teeth, the more likely those teeth are to be worn regardless of their location in the mouth. Second, and more important, is that *Stiner* (1998) is aware that teeth in different positions in the ursid mouth erupt and wear at diverse rates, and she accounts for

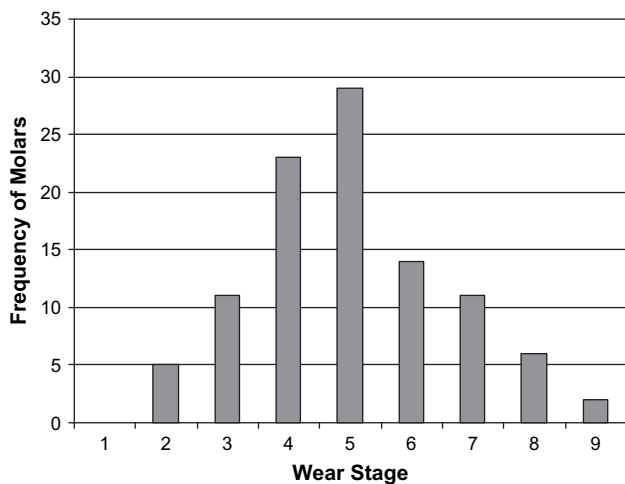


Fig. 4. Frequencies of ursid molars from Lawson Cave and Jerry Long Cave assigned to *Stiner's* (1998) wear stages.

this in her wear schedule. Indeed, the wear schedule is not perfect, but that is why she clearly states that it should be used at ordinal scale with the notable exception of these discrete life-history markers (e.g., eruption of permanent molars).

Each tooth is assigned to one of nine wear stages using *Stiner's* (1998:312–313) wear-chart illustrations, and then those data are aggregated into three life-history periods—juveniles, prime adults, and old adults. This three-period format is useful for three reasons: first, it reduces sampling requirements such that fewer specimens per assemblage are needed to recognize differences in mortality patterns; second, the periods reflect meaningful life-history phases based on the prime-adult class approximating the “reproductive years”; and third, the technique is suited to graphing on a three-pole diagram, which allows direct visual comparison of multiple mortality patterns (see *Stiner*, 1990, 1994 for more details). *Stiner's* (1990, 1994, 1998) three-phase aging system requires a sample size of roughly a dozen individuals per assemblage; histogram mortality patterns are more representative when samples approach thirty individuals (*Lyman*, 1987). There were 10 bears from Lawson Cave and 12 from Jerry Long Cave. The samples are treated independently using the three-phase system, and they are aggregated when considered in histogram format.

Taphonomy

It is not possible to directly consider absence of juveniles from these cave assemblages. However, it is possible to consider the taphonomic conditions that would have fragmented relatively low-density, friable juvenile remains (bones and teeth) to the point that they would not have been recovered or identified. Such a taphonomic consideration is important because the argument presented in this paper rests firmly on the judgement that juvenile ursid remains are not as regularly deposited in these natural traps as are those of young adults. This pattern would not be expected if natural traps captured a random sample of ursids from stable living populations, which are dominated proportionally by juveniles.

The ursid remains from both caves are extensively fragmented in that most of the limb elements were green fractured, which is to be expected in samples created by steep falls into natural traps (e.g., *Wolverton*, 1996, 2001), yet this is not a taphonomic event that would have rendered juvenile remains absent from these faunas. It is more important to gauge whether or not post-depositional taphonomic processes occurred that are likely to crush or pulverize bone to the point of non-recovery and non-identifiability. For example, should ursids have survived the fall and lived for short periods of time in the trap chambers, they would likely have trampled and consumed bone. For this reason, it is important to determine whether or not there is a signature of intense fragmentation processes on remains from the caves. This is not a direct analysis of juvenile tooth and bone fragmentation, which is impossible because they are absent from these samples, but it is a consideration of taphonomic processes likely to pulverize bone, which would have had an important effect on

juvenile remains should they have been present and then destroyed in the caves.

A variable directly relevant to these processes is “intensity of fragmentation,” which can be measured using a ratio of NISP to MNE (Lyman, 1994b). If faunal remains of small and large taxa deposited in the cave are intensely fragmented, then processes like trampling and heavy carnivore gnawing are likely to have occurred. If such ended up being the case, then the taphonomic history of these faunas is such that juveniles might have been deposited and are only analytically absent; thus, the integrity of the observed mortality patterns would come into question.

NISP:MNE for ursid and cottontail (*Sylvilagus floridanus*) limb bones is used to evaluate the effects of fragmentation on the Jerry Long and Lawson Cave assemblages. The purpose of analyzing remains from both taxa is to compare intensity of fragmentation across taxa of two different body sizes. Cottontails are small bodied and have low-density elements that are more susceptible to pulverization than those of ursids. Ursid elements are large and relatively dense. MNE is calculated by determining whether or not specimens overlap anatomically; for example, if one proximal femur fragment overlaps with one distal femur fragment, then $MNE = 2$. If the fragments do not overlap, then $MNE = 1$. The use of an NISP to MNE ratio simply addresses the question, of the remains identified (NISP), what is the minimum number of elements (MNE)? If NISP:MNE is high, it means there are many fragments per recognizable element, and as a result pulverization might have removed low-density juvenile skeletal parts, including teeth, from the fauna. However, if NISP:MNE is low, then it is unlikely that agents of fragmentation (e.g., carnivore gnawing, trampling, rockfall) rendered low-density skeletal parts (like those of juveniles) unrecoverable or unidentifiable (Wolverson, 2001).

Another way to evaluate the effects of destruction on an assemblage (e.g., carnivore damage) is to compare the abundances of high- and low-density long-bone ends. This is accomplished using ratio values (RVs), which are calculated by “determining the MNE for the proximal end and for the distal end of each bone, and then dividing all four values ([e.g.,] proximal humerus, distal humerus, proximal tibia, distal tibia) by the largest of four values” (Lyman, 1994a:400). If low-density ends are missing or of low abundance, presumably because they are differentially prone to taphonomic destruction, then low-density juvenile remains might also have been destroyed. In such a case, the absence of juvenile remains would be a product of an assemblage’s taphonomic history and not the result of juveniles never having been deposited.

RVs are plotted as to whether they fall in a “zone of destruction” or a “zone of no destruction,” which were derived by Binford (1981) from observation of assemblages that are known to have been damaged or undamaged by carnivores (see Lyman, 1994a:398–402). Carnivore-ravaged assemblages produce RVs that are plotted in the zone of destruction, which reflects low abundance of low-density proximal ends. Infrequent occurrence of carnivore damage and evenly distributed proportional abundance of high- and low-density long-bone

ends, in this case tibiae and humeri following Binford (1981) and Lyman (1994a), would suggest that density-mediated destruction was not an important factor in a fauna’s depositional history and supports the interpretation that juveniles simply were never trapped in the caves.

Results

Ursid mortality in natural traps

Both cave faunas produce ursid age structures that are dominated by prime adults (Table 4). Seventy-one percent ($n = 29$) of the molars from Jerry Long Cave and eighty percent ($n = 47$) from Lawson Cave are assigned to wear stages four to seven, which are included in the prime-adult life-history period. Further, 51% ($n = 51$) of the teeth from the samples are age-scored as *young* prime adults (in wear stages four and five). Data from the cave samples are aggregated to form the histogram in Figure 4, but they are considered separately in the three-pole graph (Fig. 5). Included in Figure 5 is a cave-bear (*U. deningeri*) assemblage from Yarimburgaz Cave, Turkey—the ursid mortality pattern from Yarimburgaz Cave exhibits a high proportional abundance of young and old individuals suggesting that it represents a hibernation death assemblage (Stiner, 1998). This mortality pattern is markedly different from the natural-trap patterns.

The age structure of Late Holocene ursids within Missouri is unknown, but here mortality patterns are considered in contrast to the living-structure model discussed by Lyman (1987) (Fig. 1) in order to (1) show that natural-trap mortality differs from the model, and (2) to demonstrate that it is unlikely that these natural-trap mortality patterns resulted from random capture of ursids. Theoretically, living populations have high

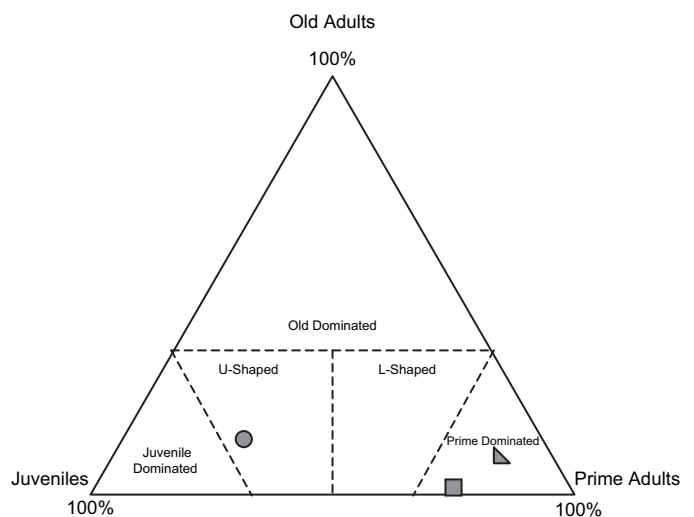


Fig. 5. Three-pole diagram illustrating ursid mortality patterns from Yarimburgaz Cave (circle) (Stiner, 1998), Lawson Cave (triangle), and Jerry Long Cave (square) as well as areas where L-shaped, U-shaped, and old-, juvenile-, and prime-dominated mortality patterns fall within the graph (after Stiner, 1990, 1994, 1998). Yarimburgaz Cave is interpreted as resulting from natural hibernation deaths; the other two caves are natural-trap assemblages.

frequencies of juveniles; mortality that reflects living structure should be relatively L-shaped (Lyman, 1987, 1994a; Stiner, 1990). Wolverton (2001) demonstrates that it is unlikely that prime-dominated mortality at Lawson Cave resulted from random capture of ursids. Data from Jerry Long Cave, when combined with those from Lawson Cave, support that argument. Spearman’s Rho comparing the rank-ordered proportional abundances of Lyman’s living-structure (L-shaped) model (Fig. 1) to the natural-trap age-class distribution (Fig. 4) indicates that the two patterns do not correlate to one another, i.e., they are distinct from one another ($R_s = -0.1$, $p = 0.797$). Clearly, ursid mortality in these natural traps is neither U-shaped nor L-shaped but something entirely different—it is prime dominated (Figs. 4 and 5).

Taphonomy of two natural trap faunas

Although ursid mortality is prime dominated at Lawson Cave and Jerry Long Cave, other taphonomic factors, such as differential fragmentation and density-mediated destruction of bone, could produce such a pattern. Juvenile skeletons tend to be of lower structural density than those of adults and thus susceptible to damage (Lyman, 1985, 1994a); therefore, it is necessary to demonstrate that the low abundance of juvenile remains is unlikely the result of density-mediated destruction or pulverization via such factors as trampling or carnivore gnawing but instead the result of their absence from the fauna. Cottontail-rabbit and black-bear limb bones from both caves are not intensely fragmented; there are fewer than two fragments per element (Table 5). It does not appear that the high proportional abundance of prime-adult teeth is the result of intense fragmentation producing under-representation of juvenile teeth.

Other lines of evidence also indicate that juvenile teeth are absent from the sample because members of the age class were not trapped in the caves. Carnivore damage on ursid remains from both caves is rare; of the 83 identified long-bone specimens from Jerry Long Cave, only 19 (23%) exhibit light carnivore damage and none are severely damaged. The Lawson

Cave ursid remains similarly exhibit a low occurrence of carnivore damage (Wolverton, 2001).

RVs from Jerry Long Cave ursid and cottontail remains (Table 6) fall within or near the zone of no destruction (Fig. 6). The ursid humerus RV falls outside of the zone of destruction because low-density proximal ends are more frequent than high-density distal ends, a scenario that was not encountered by Binford (1981) and that is not accounted for in the RV model. The cottontail humerus RV also falls outside the zone of no destruction, but proximal ends are not sufficiently under-represented to produce a value within the zone of destruction. The RVs indicate that density-mediated destruction produced only minimal effects on the frequencies of skeletal parts making up the Jerry Long Cave fauna. Low-density tibia and humerus ends tend to occur at similar abundances as high-density ends at Lawson Cave as well (Table 6; Fig. 6). Prime-dominated ursid mortality at Jerry Long Cave and Lawson Cave is unlikely the result of differential fragmentation or density-mediated destruction rendering juvenile remains unidentifiable or absent from these assemblages.

Discussion

The implication that prime-aged adult bears are more likely to be entrapped in shaft caves than individuals belonging to other age classes is provocative for two reasons. The first reason is that trapping of these Missouri bears occurred during a time when competition for space between humans and black bears intensified dramatically—the historic period. A decrease in available habitat likely affected young bears severely because it is this age group that is limited by intraspecific competition for food, size of home ranges, and access to mates (e.g., Bunnell and Tait, 1981; Powell et al., 1997). Under these conditions, young-adult ursids establishing home ranges within a matrix of larger, more-experienced, established adults are more likely to seek food in unknown, even dangerous locations because their nutritional stress levels are high (Poelker and Hartwell, 1973; Bunnell and Tait, 1981). Thus, they are more likely to become trapped in and die in natural traps than members of other age classes. Such stress would have been amplified as human populations expanded during

Table 5
NISP:MNE for cottontail and black-bear long bones from Jerry Long Cave and Lawson Cave

	NISP:MNE Lawson	NISP:MNE Jerry Long
<i>Sylvilagus floridanus</i>		
Humeri	10:8 = 1.25	14:13 = 1.08
Ulnae	12:12 = 1.0	8:8 = 1.0
Femora	21:14 = 1.5	16:14 = 1.14
Tibiofibulae	35:22 = 1.59	20:17 = 1.18
Total	78:56 = 1.39	58:52 = 1.12
<i>Ursus americanus</i>		
Humeri	22:14 = 1.57	30:18 = 1.67
Radii	14:12 = 1.17	16:12 = 1.33
Femora	22:14 = 1.57	17:15 = 1.13
Tibiae	10:8 = 1.25	20:18 = 1.11
Total	68:48 = 1.42	83:63 = 1.32

Table 6
Ratio-value data for ursid and cottontail humeri and tibiae/tibiofibulae

	Lawson Cave		Jerry Long Cave	
	MNE	Ratio Value	MNE	Ratio Value
<i>Ursus americanus</i>				
Distal tibia	9	0.82	8	0.44
Proximal tibia	8	0.73	7	0.38
Distal humerus	11	1.00	12	0.66
Proximal humerus	8	0.73	18	1.00
<i>Sylvilagus floridanus</i>				
Distal tibiofibula	21	0.95	13	1.00
Proximal tibiofibula	22	1.00	12	0.92
Distal humerus	15	0.68	13	1.00
Proximal humerus	19	0.86	8	0.62

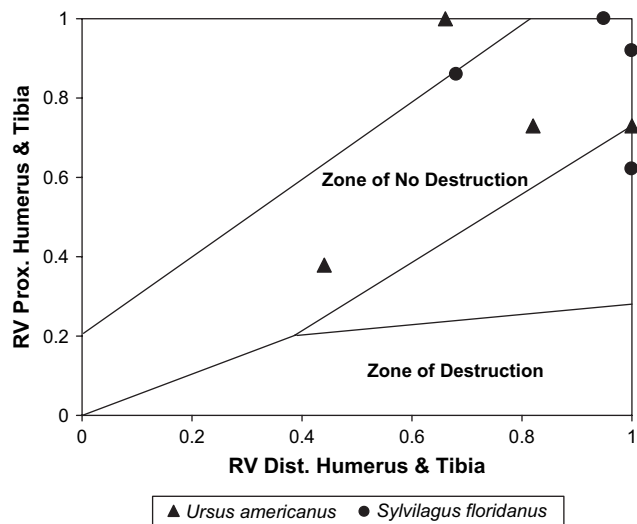


Fig. 6. Lawson Cave and Jerry Long Cave destruction graph: The RVs of ursid and cottontail tibiae/tibiofibulae and humeri illustrate that low-density proximal ends occur in the sample. The RVs fall within or near Binford's (1981) observed "zone of no destruction."

the historic period in Missouri, and eventually black bears were indeed extirpated from the state and much of the American Midwest.

Setting up this historical example as an analog enables formulation of a test implication for the Kurtén Response hypothesis, which is the second reason these North American paleontological data are of interest. Grayson and Delpech (2003) clearly document that the abundance of cave-bear remains decreases with increasing evidence for habitation by *Homo* sp. in European caves (see also Straus, 1982; Stiner et al., 1996; Clark, 2002). They suggest that broader Late Pleistocene demographic trends among human populations might have pressured cave bears to extinction. An important resource that would have been compromised for cave bears should human populations have grown during the Late Pleistocene is available habitat including caves as den sites but also available home-range space. The setting is very similar to historic-period Missouri because the state is littered with caves and because human use of available habitat intensified during the historic period. At least two natural traps captured prime-dominated samples of black bears under these circumstances.

Direct competition between cave bears and hominins need not have occurred for hominins to have contributed to the cave bear's extinction. It is perhaps more romantic to envision bears and humans directly competing for, say, cave sites, but competition at a much coarser scale would have been more important. At issue is niche breadth at the evolutionary scale (e.g., Hutchinson, 1959; see discussion and references in Stiner, 1994), and what is important here is that hominins became increasingly more present on the European landscape during the Pleistocene. Further, cave bears, much like modern bears, would have required large amounts of space, and the presence of another habitat-consuming, highly skilled omnivore, hominins, may have been enough to tip the scale of evolution against the cave bear. Certainly, there is a potential reflection

of this process in the zooarchaeological and paleontological records because cave-bear remains become less abundant as hominin presence increases through time (e.g., Grayson and Delpech, 2003). However, this single line of evidence reflecting such a correlation would be greatly amplified in its importance should another be added to the argument. Another potential line of evidence is to consider cave-bear mortality in natural traps that date to the Pleistocene. How many cases would be needed? Perhaps a few spanning the period when hominins increasingly occupied cave-bear habitat and likely competed for niche space. There is no doubt that modern humans have competed directly with modern ursids for niche space and habitat; incidentally, the larger the bear, the more fierce the competition it has with modern humans for survival. Cave bears were very large ursids; thus, competition between them and hominins for habitat may have been intense.

To test Kurtén's hypothesis that humans out-competed cave bears to the point of extinction, Grayson and Delpech (2003) suggest that multiple cases of declines in cave-bear-remain abundance in European Late Pleistocene assemblages need to be observed. Another appropriate test is to examine natural traps that date to the Late Pleistocene to determine whether or not they are dominated by the remains of young-adult cave bears. Further, because members of the young-adult age group are more likely to die in natural traps than bears in other age classes, it can be expected that the proportion of young-adult ursids should increase in natural-trap faunas during the Late Pleistocene. A test of this implication might include studying such faunas dating to the Lower, Middle, and Upper Paleolithic cultural periods of the Late Pleistocene. As the presence of humans (*Homo* sp.) became more prominent, so too should have competitive stress on cave bears, which represent an omnivore that would have competed directly with humans for caves and potentially for other types of habitat. Thus, natural-trap ursid mortality should be expected to have become progressively more prime dominated as human populations grew during the Late Pleistocene.

One Late Lower Paleolithic (after 300,000 years ago) cave-bear (*U. deningeri*) assemblage that appears to exhibit a young-adult-dominated mortality profile is from Sima de los Huesos in the Sierra de Atapuerca karst system of north-central Spain (García et al., 1997; Wolverson, 2001; Fig. 7). The aging schedule used to record the mortality pattern is published in García et al. (1997; see also Wolverson, 2001), and it is different from the schedule used here. However, the mortality pattern is not U-shaped, nor does it exhibit a high abundance of individuals with deciduous teeth (Fig. 7). It might be prime dominated like those from Jerry Long and Lawson Caves, but that interpretation cannot be made confidently unless the assemblage is re-evaluated using Stiner's wear schedule. It appears from García et al.'s (1997) description of their schedule that Stiner's (1998) division between juveniles and prime adults would fall somewhere in the middle of stage I and that the prime-adult stage would end somewhere early in stage III; if this is truly the case, then the assemblage is proportionally abundant in young adults. Even using García et al.'s (1997) schedule, the pattern is clearly not U-shaped.

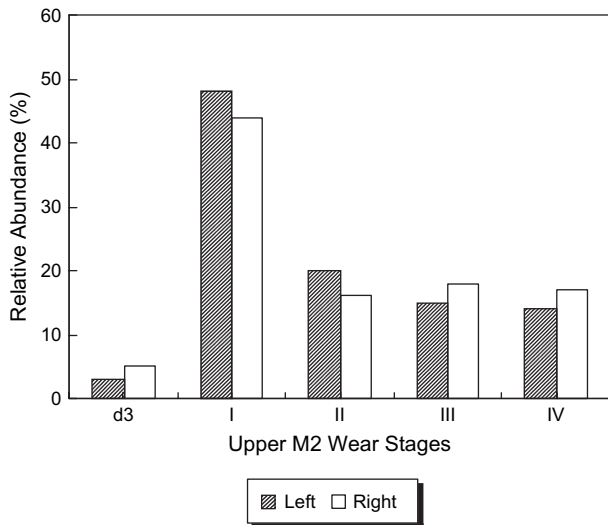


Fig. 7. Cave-bear mortality profile from Sima de los Huesos (after Garcia et al., 1997: 167–168).

The low abundance of individuals with deciduous teeth suggests that it might not be L-shaped either.

Cave-bear and hominin (*Homo* sp.) remains co-occur at Sima de los Huesos in a pit deposit (Arsuaga et al., 1997). The ursid mortality pattern appears to be similar to those described in this analysis from North America (but see discussion above), and the pit's structure is that of a deep natural trap (Arsuaga et al., 1997; Garcia et al., 1997). The pit is different than either Lawson Cave or Jerry Long Cave in that it is deep within a larger karst system and the trap is several hundred meters in depth. Hominins either entered the cave intentionally through the existing vertical entrance, through unknown horizontal entrances, or were accidentally trapped (see discussion in Andrews and Fernandez-Jalvo, 1997). Andrews and Fernandez-Jalvo (1997) discuss the cave-bear fauna as an enigma. They suggest that natural traps should not selectively accumulate carnivores; Lawson Cave trapped herbivores, but the assemblage is dominated by carnivores (Table 2). One of the most abundant herbivores in the assemblage is the domestic pig (*Sus scrofa*), which eats carrion. In Jerry Long Cave, several carnivores are relatively abundant, and the remains of a carrion scavenger, the turkey vulture (*Cathartes aura*), are common. Carrion in the bottom of natural traps likely attracts meat eaters. More important is that Sima de los Huesos is deep within a karst system where carnivores are more likely to travel than are herbivores. Further, fall survivors would have damaged and destroyed some bones in the deposit, which might explain some of the taphonomic characteristics of the faunal and fossil assemblages (Andrews and Fernandez-Jalvo, 1997). Sima de los Huesos has the structure of a natural trap and it accumulated a high relative abundance of species likely to be attracted to carrion (Garcia et al., 1997); at this time its status as a natural trap cannot be disconfirmed even if hominins entered through a now-destroyed entrance elsewhere in the karst system (Andrews and Fernandez-Jalvo, 1997).

If cave bears were stressed by the increasing presence of humans during the Late Pleistocene, then perhaps they accidentally fell into Sima de los Huesos when looking for den sites or in response to a carrion attractant. Either way, the deaths would have been accidental, and young adults would have been more susceptible to such deaths in that they were likely out-competed for favorable den sites and for food by established adults. Should the Sima de los Huesos cave-bear fauna be confirmed to be young-adult dominated, and should other traps dating to the Late Pleistocene in Europe exhibit similar mortality, then Kurtén's hypothesis is supported with another line of evidence. Combined with Grayson and Delpech's (2003:1644) test implication regarding cave-bear-remain abundance, such evidence would provide a provocative argument for an "anthropogenic role in the Pleistocene extinction of a large mammal on a Northern Hemisphere continent."

Conclusion

Data discussed here indicate that zooarchaeologists can expect to encounter young-adult bears in natural traps because such bears today are more likely to be under nutritional stress than bears in other age classes and, thus, are attracted to carrion in such caves. Because cave structures change through time and horizontal and vertical entrances open and close, ursid mortality data are a useful tool with which to study taphonomic histories of palimpsest European cave faunas that contain hominin and cave-bear remains. In particular, ursid mortality can be used to indicate whether bears died during hibernation or through entrapment, and most research on cave-bear mortality indicates that humans did not hunt hibernating bears upon encounter. These kinds of data are in turn of potential use in testing the Kurtén Response hypothesis incorporating the analog discussed throughout the paper.

If researchers are to evaluate the role that hominins played in the extinction of cave bears or merely the ecological implications of the interaction of the two taxa, then mortality data are important for identifying natural versus cultural accumulations and for deriving test implications for the Kurtén Response. In particular, the Kurtén Response hypothesis implies that the growing presence of hominins in Europe during the Late Pleistocene might have contributed to or even caused the extinction of cave bears. Testing this hypothesis requires more than direct association of human and cave-bear remains in a standard archaeological sense. In order to understand the effects of competition for space between bears and humans during the Late Pleistocene in Europe, a broader ecological context must be understood. Evidence of broad ecological contexts, however, is rarely if ever encountered in the archaeological and paleontological records; thus, the prehistorian must rely on analogy. Although the usefulness of behavioral analogy has been much debated in the archaeological literature (e.g., Ascher, 1961; Binford, 1967; Gould and Watson, 1982; Wylie, 1982; Wolverson and Lyman, 2000), black bears and cave bears share an evolutionary history, which strengthens the analog used in this paper.

The role that humans played in prehistoric extinction events is difficult to gauge archaeologically because direct data on interactions between hunters and their prey are not well preserved. If humans are placed within the carnivore community as a member that influences other species and vice versa (sensu Stiner, 1994), modern ecological data can play a role in understanding prehistoric extinctions via analogy. However, these behavioral analogs are of limited utility because whether or not they truly reflect prehistoric conditions is untestable and unknowable (e.g., Dunnell, 1978, 1982; Wolverson and Lyman, 2000). It is important, thus, to clearly and carefully outline such analogs and the assumptions that underlie them. Again, the strength of the analog used in this paper rests on the close behavioral and evolutionary similarities between cave bears and black bears. An obvious question is, how closely related must two taxa be in order to use such an analog? The answer depends on the comfort with which the prehistorian is willing to assert assumptions inherent in the process of analogy and the tolerance of archaeology and paleontology in general to the conclusions drawn concerning prehistoric phenomena and circumstances. Analogy, despite its problems, however, may be the only source of information on the broader ecological relationships between prehistoric humans and the species that became extinct after human dispersal into various regions of the world during the Pleistocene.

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