

CAVE BEAR ECOLOGY AND INTERACTIONS WITH PLEISTOCENE HUMANS

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Abstract: Human ancestors (*Homo* spp.), cave bears (*Ursus deningeri*, *U. spelaeus*), and brown bears (*U. arctos*) have coexisted in Eurasia for at least one million years, and bear remains and Paleolithic artifacts frequently are found in the same caves. The prevalence of cave bear bones in some sites is especially striking, as these bears were exceptionally large relative to archaic humans. Do artifact–bear associations in cave deposits indicate predation on cave bears by early human hunters, or do they testify simply to early humans' and cave bears' common interest in natural shelters, occupied on different schedules? Answering these and other questions about the circumstances of human–cave bear associations is made possible in part by expectations developed from research on modern bear ecology, time-scaled for paleontologic and archaeologic applications. Here I review available knowledge on Paleolithic human–bear relations with a special focus on cave bears (Middle Pleistocene *U. deningeri*) from Yarimbuzguz Cave, Turkey. Multiple lines of evidence show that cave bear and human use of caves were temporally independent events; the apparent spatial associations between human artifacts and cave bear bones are explained principally by slow sedimentation rates relative to the pace of biogenic accumulation and bears' bed preparation habits. Hibernation-linked behaviors and population characteristics of cave bears, based on osteometric, isotopic, and age and sex structure analyses, indicate that they depended heavily on seasonal food supplies, which were rich in resistant plant materials and cryptic, gritty foods. There is little evidence of direct ecological interaction among Pleistocene humans and cave bears.

Ursus 11:41–58

Key words: brown bears, cave bears, Mediterranean, mortality, paleodiet, Pleistocene human–bear interactions, sex ratio, *Ursus arctos*, *Ursus deningeri*, *Ursus spelaeus*

Pleistocene sediments in Eurasian caves often contain complex records of habitation by predatory species. Of these, early humans (*Homo* spp.), wolves (*Canis lupus*), foxes (*Vulpes* spp.), spotted hyenas (*Crocuta crocuta*), and bears (*Ursus* spp.) were especially prolific sources of bone refuse. Making sense of cave faunas is an interesting, but also challenging, enterprise, beginning with the questions of how the assemblages formed, what species were active collectors and modifiers of bones, and the extent to which sediment chemistry favored skeletal preservation. These problems fall in the methodological domain of vertebrate taphonomy, an area of research concerned with how bone assemblages become part of the paleontological and archaeological records.

While clear answers about assemblage formation history seldom are easy to obtain, there is a wealth of information locked in cave sites about the ecology of early humans and their relations with potential competitors, mainly of the order Carnivora. The story of human–bear interactions is both important and enigmatic. Converging patterns of omnivory would seem reason enough for Pleistocene humans and bears to have stayed out of each other's way. Yet the remains of cave bears or brown bears are found in nearly every Eurasian Middle and Upper Paleolithic site with preserved bone—sometimes many bear bones, but more usually a few. In fact, bear remains turn up in Paleolithic cave sites more consistently than the remains of almost any other large carnivore, at least prior to 20,000 years ago, when greater interspecific exclusion among cave residents is apparent (Gamble 1986, Stiner 1994).

By way of anthropological background, the chronology of Paleolithic cultures begins around the Plio-Pleistocene boundary and lasts until the Holocene. The Paleolithic traditionally is divided into 3 major cultural phases: the Lower, the Middle, and the Upper Paleolithic. The hominid forms associated with these cultures varied considerably, and there is no simple correspondence between cultural (behavioral) change and hominid morphological (skeletal) change. Lower Paleolithic artifacts are attributed to some of the late Australopithecine species, which were confined to the African continent, as well as to early variants of the genus *Homo*, which by 1.4–1.8 million years ago (MYA) spread from Africa into much of Eurasia. First appearing some 250,000 years ago, Middle Paleolithic artifacts are characterized by innovations in stone tool production techniques and artifact forms. They are attributed to archaic humans such as Neandertals in general (*H. sapiens neanderthalensis*) as well as to earliest anatomically modern humans (*H. sapiens sapiens*) in the west Asian cave sites of Qafzeh and Skhul (Bar-Yosef et al. 1986, Valladas et al. 1988, Bar-Yosef 1989, Vandermeersch 1989). The Upper Paleolithic, which began between 42,000 and 35,000 years ago (depending on region), is marked by spectacular radiations in material culture over a relatively short time span. Artifacts of all 3 periods commonly are found in open sites. Cave sites, usually in limestone solution cavities, were periodically inhabited during the Middle and Upper Paleolithic culture periods only, and most of the archaeofaunal records of these periods come from caves for the simple reason that cave sediments favor bone preservation. Paleolithic peoples probably were no more

bound to caves than bears, but both were at times attracted by the prospect of easy shelter.

Here I review available knowledge on Pleistocene human–bear relations, as gleaned by archaeological investigations of cave sites, with a special focus on cave bears in southern Europe and western Asia. The rich literature on modern brown and black bears (*U. americanus*) plays a key role in this kind of research. Specifically, wildlife data are used to build testable predictions about how bears may contribute to faunal assemblage formation. The faunal patterns inside caves that can be explained by modern bear behavior are played against anthropological hypotheses about ancient human behavior. A variety of analytic techniques are marshaled for this kind of research, including osteometry, skeletal damage analysis, taxonomic and body part profiling, and mortality and isotope analyses, to obtain rigorous, if indirect, evidence about Pleistocene cave bear (and human) ecology. For related publications see Stiner (1994, 1998) and Stiner et al. (1996, 1998), and for information on Pleistocene carnivore guilds in the Mediterranean Basin, see Stiner (1990, 1991, 1992, 1993, 1994) and citations therein.

HISTORY OF HOMINID–URSID COEXISTENCE

Between 1.8 and 1.4 million years ago, populations of a hominid known as *Homo ergaster* expanded from Africa into Eurasia. Hominids' spread across southern Asia appears to have been rapid (Klein 1989). Colonization of continental Europe and the colder regions of north-central and eastern Asia by hominids took considerably longer, but they certainly reached these regions before 500,000 years ago. The first hominids to enter Eurasia were omnivores with a notable capacity for hunting vertebrate prey, a property which may have been essential to winter survival in northern habitats (Foley In Press, Stiner In Press). Colonization of new continents put hominids in contact with diverse environments and novel floras and faunas.

Hominids were late arrivals to the predatory guilds of Africa, where they first evolved, and hominid–carnivore interactions must have intensified as meat-eating exposed hominids to interspecific competition. Hominids were late arrivals to predator guilds, yet again, as they invaded Eurasian ecosystems characterized by winters of intense cold, lasting snow cover, and seasonally scarce food. In addition to habitual flesh-eaters, the process of colonization brought hominids together with 2 widespread omnivorous genera of the northern hemisphere—pigs (*Sus* spp.) and bears (*Ursus* spp.). The ancestral bear of Lower-

Middle Pleistocene (*U. etruscus*) was relatively small-bodied but evolved into larger types by the Middle Pleistocene. This presentation concerns 2 bears in particular, cave bears (*U. deningeri*, *U. spelaeus*, *U. rossicus*) and brown bears (*U. arctos* and its most immediate ancestors) (Kurtén 1976, Baryshnikov 1998). Once prevalent throughout Eurasia, all cave bears were extinct by roughly 10,000 years ago (Baryshnikov 1999), and most populations disappeared considerably earlier. Brown bears continue to exist and even doubled their geographic range during the Late Pleistocene by colonizing the Americas, as did humans not long thereafter.

Because recent humans and bears display strong attractions to meat as well as to energy-rich plant foods, their evolutionary histories following biogeographic contact must have affected one another to some extent. The ecological links between humans and bears may always have been relatively weak, because both tend to be versatile, generalist foragers (sensu Foley 1984). These links were perennial, however, due to overlapping needs for foraging territory and, periodically, for shelter.

PLEISTOCENE HUMAN–BEAR INTERACTIONS: FACT AND FICTION

There is no shortage of bear stories in anthropological and popular literature. Most of them concern “cave men” (Neandertals) and cave bears. The original site for the Neandertal cave bear cult is Drachenloch Cave in Switzerland, made famous by Bächler's radical interpretation of a fauna consisting almost exclusively of bear bones (Kurtén 1976). The sediments of Drachenloch lacked artifactual material, but allegedly preserved a stone crypt with as many as 7 cave bear skulls arranged neatly inside and, nearby, a smaller stone chest packed with bear long bones. Bächler's claim was refuted by Koby (1940) and in Kurtén's (1976) highly entertaining book, *The Cave Bear Story* (also Kurtén 1958, 1971, 1973).

The cave bear cult is an engaging story, if only for the early spiritualism it implies. The idea that archaic humans manipulated bear remains in symbolic ways persists, at least partly because bear bones frequently occur with stone artifacts in other Paleolithic cave sites. Cut marks or burning damage have been found on a few bear bones in Middle and Upper Paleolithic sites (Barta 1989, Stiner 1994:109–123), although examples are rare overall. Bear images also figure in the earliest known art of the Upper Paleolithic in western Europe, but these cases date to no earlier than 32,000 years ago (Chauvet et al. 1996). Many sedimentary associations of bear bones and Paleolithic stone artifacts are much older, and one of the oldest examples of all comes from Yarimbuz Cave,

Turkey.

In 1992 I was invited by F. Clark Howell (University of California-Berkeley) and Güven Arsebük (Istanbul University) to work on a large, well-preserved fauna that they had excavated from the Middle Pleistocene layers in Yarimburgaz Cave. The site is >250,000 years old (Blackwell et al. 1990, Farrand 1992, Kuhn et al. 1996, Stiner et al. 1996, Santel and von Koenigswald 1998), dating to well before the appearance of anatomically modern humans or Upper Paleolithic cultures anywhere in the world. The formation history is complex, and the deposits are rich in cave bear remains (*Ursus deningeri*) (Table 1) and just under 1,700 Paleolithic stone artifacts (Fig. 1; Kuhn et al. 1996). Also present in low frequencies are fragmentary remains of a diverse array of ungulate and non-ursid carnivore species (Table 2).

Only a few of the ungulate remains have cut marks (<1%) from Paleolithic stone tools. Gnawing damage is present on many more of the ungulate bones as well as on bear and non-ursid carnivore bones (Fig. 2). Bear remains were least affected by gnawing carnivores, however, and they are the only remains that were also gnawed significantly by small rodents (Table 3). Stone artifacts

Table 1. Specimen counts by general taxonomic groups represented in the Middle Pleistocene deposits of Yarimburgaz Cave.

Mammal group	Total identified skeletal specimens	%
Herbivores	151	4
Bears	3,920	93
Other carnivores	109	3
Total	4,180	100

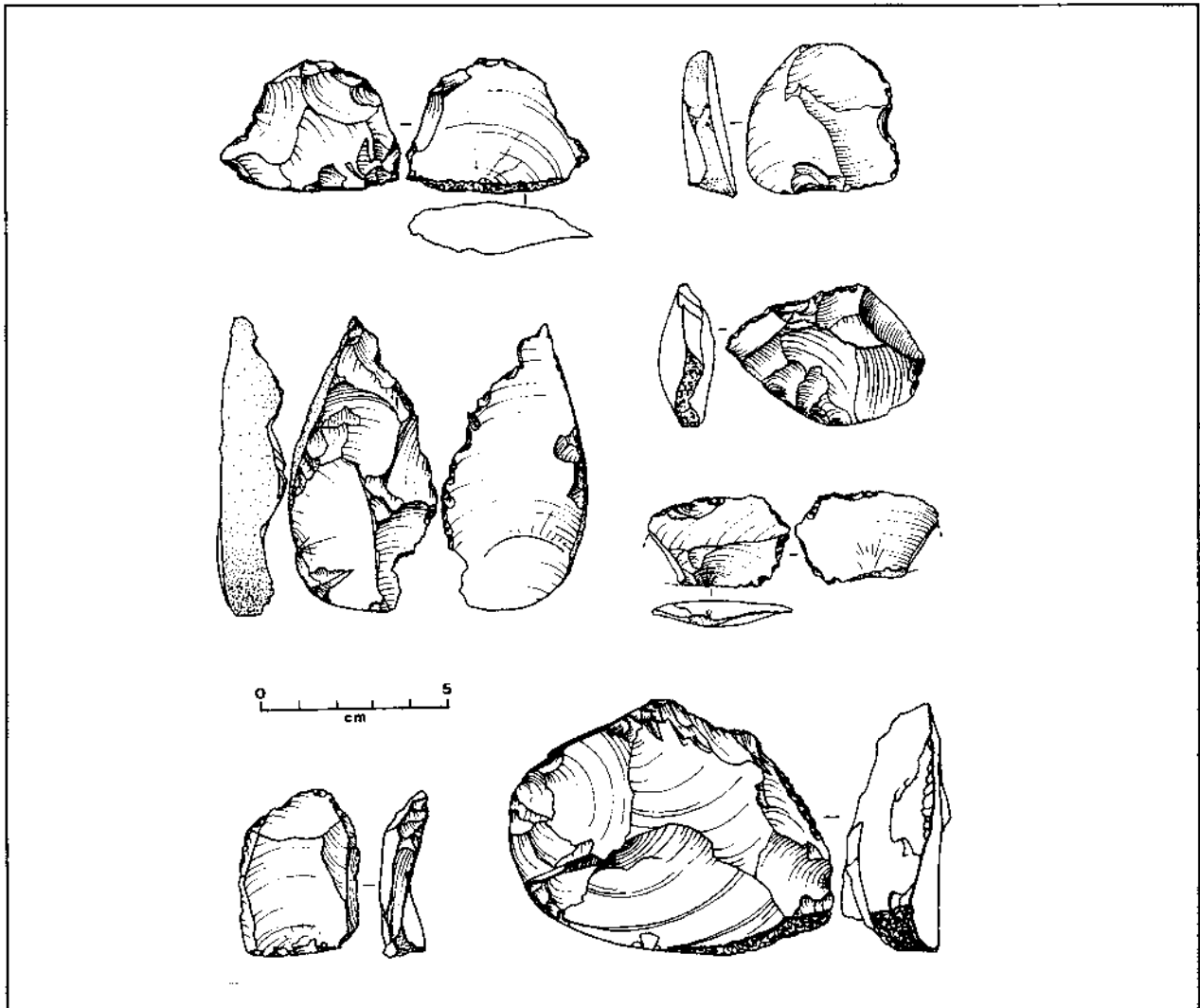


Fig. 1. Examples of Paleolithic stone tools from Yarimburgaz Cave (from Kuhn et al. 1996 with permission of M. Stiner).

Table 2. Macromammal specimen counts by genus or body size category from the Middle Pleistocene deposits of Yarimburgaz Cave.

Taxon	Total specimens identified
Cervidae (genus unknown)	36
<i>Cervus</i>	29
Large ungulate	17
<i>Capreolus</i>	13
<i>Dama</i>	13
<i>Equus</i>	9
Megafauna	6
<i>Bos</i> or <i>Bison</i>	5
<i>Capra</i>	5
Medium mammal (mostly ungulates)	5
<i>Sus</i>	4
Medium ungulate	3
Small ungulate	2
<i>Megaloceros</i>	2
<i>Hippopotamus</i>	2
<i>Ursus</i>	3,372
Large mammal (mostly bears)	548
<i>Panthera</i>	30
<i>Canis</i> or <i>Cuon</i> (?)	25
<i>Vulpes</i>	17
<i>Felis</i>	13
<i>Carnivora</i> (genus unknown)	9
Small mammal (mostly small carnivores)	9
<i>Mustela</i>	4
<i>Crocota</i>	2
Total	4,180

and the bones of bears, ungulates, and non-ursid carnivores are scattered together in the Middle Pleistocene layer (Fig. 3, Table 4). The candidates responsible for bone collection and modification in this site are hominids, wolves, spotted hyenas, and cave bears. Signs of each candidate are evidenced by the presence of stone artifacts or skeletal representation in the species profile.

INTERPLAY BETWEEN RESEARCH ON MODERN AND PLEISTOCENE BEARS

One of the most troubling questions about the Yarimburgaz Cave assemblage is why so many bear bones occur with the Paleolithic artifacts. One hypothesis proposes that the bear deaths resulted from non-violent causes in the context of hibernation, implying that bears' presence in the cave was not linked in time to human activities there. Alternatively, the bears may have been hunted by humans, among other predators, implying that

Table 3. Frequencies of gnawing damage from carnivores and rodents on ungulate, bear, and other carnivore remains.

Animal group	<i>n</i>	Gnawed by (%)	
		Carnivores	Rodents
Ungulates	117	23	6
Bears	3,129	10	11
Other carnivores ^a	67	18	1

^a Consists primarily of *Panthera*, *Felis*, *Canis* and *Vulpes*.

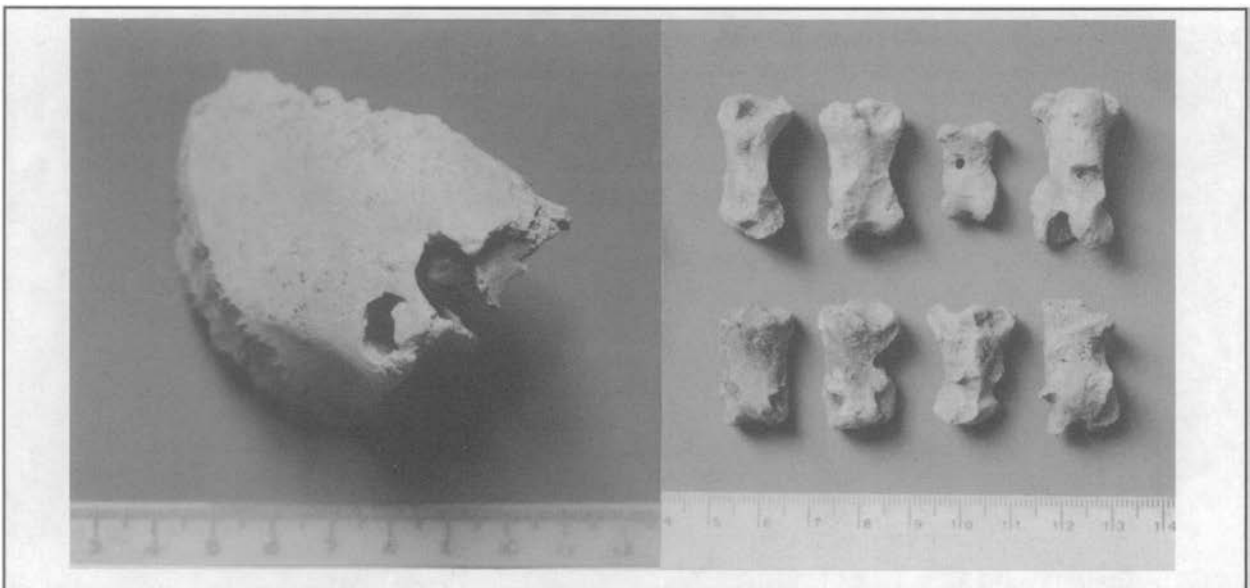


Fig. 2. Gnawed cave bear remains: frontal bone fragment of a young individual punctured by the incisors of a large adult bear (left); phalanges extensively gnawed by small rodents (right), suggesting that these bones lay undisturbed on the cave floor for some time before burial in sediment. Scale in cm.



Fig. 3. Cave bear bone and Paleolithic artifact scatter exposed during the 1988–90 excavations of the Middle Pleistocene layers in Yarimburgaz Cave (Stiner et al. 1996).

Table 4. Pearson correlation matrix of the abundances of bear, other carnivore, and ungulate remains and lithic artifacts across 17 excavation units in the Middle Pleistocene layer of Yarimburgaz Cave.

	Bears	Other carnivores	Ungulates	Lithic artifacts
Bears				
Other carnivores	0.750			
Ungulates	0.722	0.754		
Lithic artifacts	0.627	0.625	0.264	

the spatial proximity of bear bones and stone artifact belies a temporal and causal link between them.

To address these hypotheses, one first needs to know (1) whether cave bears were hibernators, and, if so, (2) whether bears would collect bones of prey in dens, and (3) the likelihood that bears would use caves for either purpose. Constructing test implications for these and other propositions begins by necessity with information on modern bears (Stiner et al. 1996, 1998; Stiner 1998). *Ursus deningeri* is extinct, of course, but some of the behavioral tendencies documented for modern *Ursus* help establish what was possible in the past. The material correlates of these behaviors can also be modeled over the long term. Important aspects of cave bear ecology are expressed by the isotopic contents of tooth enamel, patterns of bone damage, skeletal element representa-

tion, and element completeness. Information on the dominant causes of death and feeding habits can be inferred from the mortality pattern (age structure) of the fossil population based on tooth eruption, wear, and breakage. Adult sex ratios and size dimorphism between the sexes can be determined from osteometric measurements.

Models in the Absence of Complete Analogs

Cave bears, an extinct subgenus (*Spelearctos*) of Ursidae, were versatile enough to inhabit large areas of Eurasia during the Middle and Late Pleistocene. Yet cave bears had evolved a specialized dentition with large chewing surfaces and powerful chewing muscles. Their multi-cusped, bunodont dentitions emphasized crushing and grinding functions and imply a heavy dietary reliance on tough, fibrous plant foods (Koby 1940, Kurtén 1976:11–26, Baryshnikov 1998, Stiner et al. 1998). Isotope studies have yielded conflicting results on cave bear diet, however (Bocherens 1994, Hilderbrand et al. 1996, Stiner et al. 1998). Much of the controversy stems from contradictions that taphonomic and morphologic evidence pose to the isotope results (Mattson 1998, Stiner et al. 1998). It is likely that cave bear habits varied in

response to environmental circumstance, but the limits on their abilities to do so remain unknown. Pleistocene cave bears shared with other bears a general tendency toward omnivory, but their dental adaptations reached a morphologic extreme and testify to a great dependence on seasonal plant foods. This fact, along with the oft-noted prevalence of cave bear skeletons in the Pleistocene sediments of Eurasian caves, make a strong case for cave bears as hibernators (Kurtén 1958, 1976).

Although distinct species, modern black and brown bears have much in common biologically, including hibernation behavior and its nutritional and reproductive contingencies (Garshelis and Pelton 1980; Johnson and Pelton 1980; Nelson et al. 1980; Rogers 1981, 1987; Tassi 1983; Murie 1985; Clevenger et al. 1987; Clevenger 1990, 1991; Hellgren et al. 1990; Clevenger and Purroy 1991). These basic similarities permit a few generalizations about the relations between bear diet and hibernation behavior, hibernation-related mortality, and the criteria governing den site choice. The metabolic and reproductive aspects of hibernation in modern bears are thought to be intrinsic (Johnson and Pelton 1980, McNamee 1984:253–257, Watts et al. 1987, Watts and Jonkel 1988, Hellgren et al. 1990). We may assume that these qualities are unlikely to have been profoundly different in Middle and Late Pleistocene cave bear populations. The mortality that normally accompanies hibernation in bears therefore should be comparable as well.

Do Bears Den in Caves?

Even if one accepts that cave bears were hibernators, we are left to explain their presence in caves. The abilities of modern bears to make artificial shelters are well known, and excavated dens are the norm in many study areas (e.g. Rogers 1981, Kolenosky and Strathearn 1987, Schwartz et al. 1987, Mack 1990, Miller 1990, Hayes and Pelton 1994, Smith et al. 1994). However, wildlife studies from Europe and North America show that modern bears willingly hibernate in natural caves and fissures where these conveniences are present (Murie 1985:133–135, Clevenger and Purroy 1991:113–123, Hayes and Pelton 1994). The prevalence of bear remains in Pleistocene cave sediments is not necessarily explained by heavy use of them over earthen dens in the past; limestone caves and fissures are merely better preservation environments for the bones of deceased bears.

Do Bears Collect Bones of Prey in Dens?

Carnivore species that rely on natural or excavated shelters seem to divide into 2 behavioral categories: bone-collectors and non-collectors. Many of the canids and

hyaenids deliberately gather bones at den and rest sites (Mech 1970, Kruuk 1972, Ewer 1973, Fentress and Ryon 1982) and may amass great quantities of prey bones in some cases (Hill 1980, Binford 1981). Hominids did essentially the same at residential sites during the Pleistocene, sometimes in caves. The habits of bears are quite different, however. Wildlife accounts show that black and brown bears do not normally carry food of any sort to dens, and they consume little food while preparing their winter beds (McNamee 1984, Rogers 1987:23). Bears often mound piles of inedible vegetation in hibernation dens (McNamee 1984:252–253, Murie 1985:133–135, Manville 1987, Rogers 1987:20–22, Clevenger 1991, Smith et al. 1994), but bones other than those of unlucky bears generally are not found.

The location of a den is secret (Kolenosky and Strathearn 1987, Mack 1990, Hayes and Pelton 1994), because sleeping bears are vulnerable to attack despite their great size (Kurtén 1976, Tietje et al. 1986, Rogers 1987:53, Ross et al. 1988). Predation on denning bears by wolves, humans, and other bears is well known, as is cannibalism within and between bear species (LeCount 1987, Mattson et al. 1992). Food debris in and around dens would betray the location of a hibernating bear to predators and presumably conflicts with the bear's need to remain hidden. The only exception to this generalization that I have found is reported by Rogers (1987:23), a single case in which a lactating female black bear found a deer carcass near her den in spring and dragged it into the den. It is reasonable to generalize, therefore, that the quantities of non-bear bones that might accumulate in bear dens are nominal, if perceptible at all, from a paleontological point of view.

Yet the bones of a variety of large mammals *are* found in Pleistocene cave sites that also contain the bones of bears. This is true of Yarimburgaz Cave, for example, a fact which is explored in some detail below. Information on modern bear behavior nonetheless suggests that other species must be responsible for the presence of non-ursid bones. The presence of scant remains of canids and hyaenids in the Yarimburgaz species profile is quite significant in this regard.

BEAR BODY PART PROFILES AND BONE DAMAGE PATTERNS

Bears are likely to contribute their own remains to the sediments in hibernation dens, even if new bodies are added only sporadically over many generations of bears. In these circumstances all of a bear's skeletal parts should be present in an earthen or rock shelter, because the bear dies in place. The situation is quite different for large

mammal body parts ported to the shelter by carnivorous occupants, because these food items are obtained elsewhere, are divisible, and are subject to transport costs. Body parts normally are moved to safe havens piece-meal by predators such as wolves and hyenas (Stiner 1991, 1994). Although herbivores are the principal prey of large carnivores, inter- and intra-specific aggression nearly guarantees that parts of some carnivore carcasses will accumulate along with herbivore bones in the dens and rest sites of hyaenids and canids. If the site is used for reproductive purposes, the skeletons of young canids or hyaenids may also become part of the paleontologic record, though seldom as complete bodies (Stiner 1994).

Unless a bear carcass is extensively fed upon, its skeletal parts should remain inside the cave. However, bear skeletons in den sites may not stay in articulatory order, because any bear that later dens in the cave would renovate the bedding area (Reynolds et al. 1976, Judd et al. 1986). The scale of this kind of disturbance hinges on the frequency with which a shelter is re-used by bears and the rate of sediment accumulation (Kurtén 1976, Stiner 1994, Stiner et al. 1996). In the Middle Pleistocene layer of Yarimburgaz Cave, the total bear assemblage computes to a pattern of nearly complete skeletons, but the components of these skeletons are scattered in a nearly random fashion. The remains of ungulates and non-ursid carnivores are far less complete and also scattered (Stiner et al. 1996).

Gnawing damage on the bear bones, though less frequent than on other large mammal remains, suggests additional reasons why bear remains are scattered throughout the Middle Pleistocene layer. Denning bears that perish from predation may be fed upon by their attackers. But the decaying body of a bear that died from nonviolent causes will attract scavengers, often the same species known to attack bears in other circumstances. It therefore is difficult to distinguish between deaths resulting from attacks on live, dormant individuals from post-mortem scavenging on the basis of gnawing damage. Many of the gnawing traces can be attributed to wolf- or hyena-sized carnivores and, less often, to larger bears (Fig. 2).

The observations above raise questions about how the Yarimburgaz cave bears died, but they do not answer them. Gnawing damage on bear remains—or cut marks in other cases—is not proof of hunting. Such damage only indicates consumption or related use of carcasses. However, bear bones were less frequently damaged by carnivores than were the remains of ungulates and non-ursid carnivores, and rodent damage shows the opposite distribution. These observations lend some support to the hypothesis of temporal and causal independence be-

tween the bear remains and other materials in Yarimburgaz Cave. The mortality pattern of the bears has greater potential for distinguishing the circumstances of bone damage, specifically between hunting and scavenging contexts (Stiner 1998).

Causes of Cave Bear Mortality

It is clear from the wildlife literature that hibernation dens are places where brown and black bears occasionally die (Kurtén 1976; Garshelis and Pelton 1980; Rogers 1981, 1987). Of course, hibernating bears may perish from violent or nonviolent causes inside dens, just as they do in free-ranging contexts. Hunting of hibernating bears is well known among traditional human cultures of the 19th and 20th centuries (Kurtén 1976, Rogers 1981:69, Ross et al. 1988, Binford In Press). Bear hunting is not a common practice among any of these cultures and probably could never be so because bear populations are relatively unproductive (Craighead et al. 1976, Glenn et al. 1976, Bunnell and Tait 1981:77). Humans' ability to hunt hibernating bears with traditional technology (Binford In Press) nonetheless suggests that hunting must be considered a potential cause of bear mortality in dens in the past.

The unique biology of modern bears suggests that relatively distinct mortality (age structure) patterns will arise in hibernation dens from predominantly violent versus predominantly nonviolent causes. These differences in mortality patterns can be used to test the cave bears' connection to prehistoric human activities in the same shelter. The net expectation for the cave bear population using winter dens should resemble the living age structure of the total free-ranging population, because (1) all reproducing adult females must hibernate to rear their cubs, (2) reproductive rates in bears are low, and (3) other adult bears may also hibernate if the population is relatively vegetarian, as appears to have been true for cave bears.

The *living* age structure of bears that use hibernation dens each year therefore serves as the model for predation on cave bears by den raiders (Stiner 1998): prime-aged adult females, old adults, infants, and adolescents should be affected randomly by hunting and therefore be represented in the death assemblage in proportion to their living abundances (Fig. 4). Repeated hunting of denning bears should be indifferent to the ages of the individuals occupying dens for at least 3 reasons. First, there is little opportunity for attackers to survey individual vulnerability while hunting encrypted prey. Second, adult females normally accompany hibernating juveniles in their first, second, and even third winters of life. Finally, it seems that all members of the denning cluster

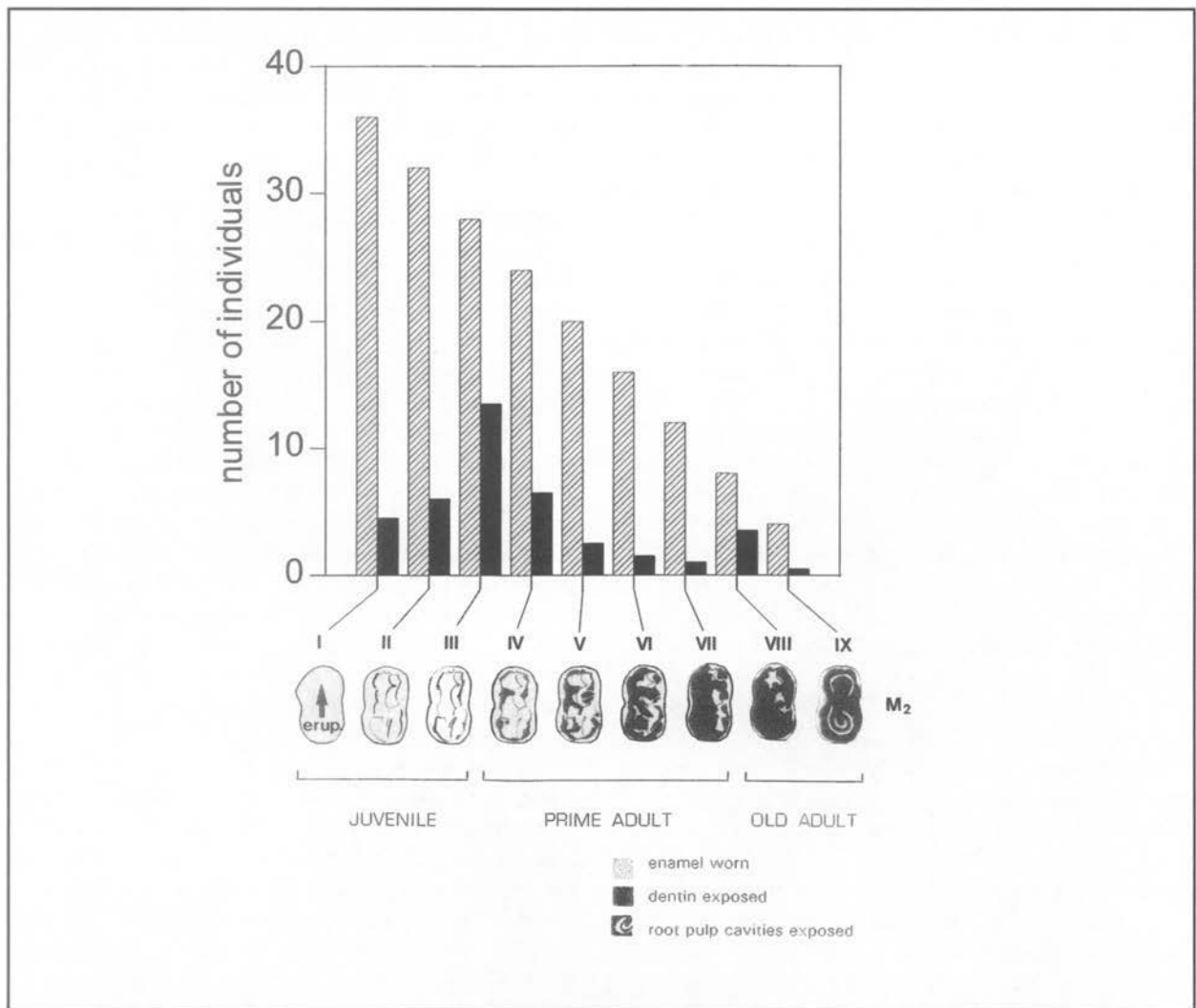


Fig. 4. Age structure of the Yarimburgaz cave bear death population (black bars) based on 9 eruption-wear stages for the M_2 molar ($n = 44$), compared to an idealized (expected, hatched bars) age structure for a hypothetical living population.

are subject to attack (Garshelis 1994), presumably because young bears are easy victims and their mothers are likely to become aggressive in tight quarters. Reports of intraspecific killing are comparatively few, but adult female bears, often with young cubs, are among the individuals that perish during den attacks (on black bears, Garshelis 1994:3; Rogers 1987). The cumulative mortality pattern resulting from attacks on hibernating bears should differ from age-dependent mortality in free-ranging bears because individual characteristics can be perceived in the latter situation and the attackers will tend to gravitate toward young, weak, and old victims. The expectation of a relatively nonselective age structure for bears attacked inside dens (though poor in adult males, Garshelis 1994, McLellan 1994) is largely theoretical, however, as too few data are currently available to con-

struct real mortality patterns with statistical confidence (Garshelis 1994).

The alternative age structure model for bear mortality in dens is the classic one of attritional death from malnutrition, disease, and senescence, a pattern typical for mammals in general (*sensu* Caughley 1977; on bears see reviews by Kurtén 1958, Stiner 1998). An attritional death pattern affects young and old age groups preferentially. Because prime-aged adults are conspicuously under-represented relative to their living abundance, an attritional mortality pattern displays a bimodal or U-shaped distribution in histograms. Non-violent mortality in modern bears is relatively high toward the end of the hibernation period if bears are in poor condition, although starvation is most common in modern populations that are not extensively hunted (Kurtén 1976;

Garshelis and Pelton 1980; Rogers 1981, 1987; McNamee 1984). Bears awaken early if their energy stores are depleted and may, as a last resort, make short forays in search of food. Females with cubs tend to stay around dens longer, both in dormancy and following first emergence in spring (Miller 1990). Starving or ill bears sometimes collapse and die in the vicinity of winter dens, although this is relatively rare (Garshelis 1994, McLellan 1994). Occasional deaths of this sort nonetheless can add up to many bodies over millennia.

The main difference between the 2 den mortality models is the near absence of prime-aged adults in the attritional (nonviolent death) model. To test the hypothesis for the paleontological cave bear population from Yarimburgaz Cave, cheek teeth were age-scored based on their eruption and occlusal wear status (Fig. 4; Stiner 1998). The Yarimburgaz cave bear sample displays an attritional (U-shaped) death pattern, exemplified by results for the lower second molar (Fig. 4). The mortality results for the Yarimburgaz bears generally support the nonviolent model of bear deaths and refute the violent model. This result, along with the complete absence of tool marks or burning damage on cave bear bones, suggest that the bear deaths in the cave were entirely independent of hominid activities there. Because the hypothesis that most of the bear deaths occurred from hunting is refuted, the possibility of a consistent temporal or causal link between cave bears and humans at this site is also refuted. Wolves or hyenas may have been responsible for a minor fraction of the bear deaths, but much of the gnawing on bear bones by hyenas and wolves appears to have occurred from scavenging.

An interesting detail of the mortality pattern for the Yarimburgaz cave bears is the pronounced peak in the late juvenile age stage III (Fig. 4). The death peak probably represents the winter when cubs became independent of their mothers. The pattern is similar to a condition noted in some modern bear populations (Glenn et al. 1976, Bunnell and Tait 1981). While the stage III peak is a relative measure and can not be tied to an exact age in real years, it suggests relatively long periods of offspring dependency, such as is seen among modern brown (as opposed to black) bears. The transition to independent life is associated with elevated mortality, often from predation by dominant adult males. Cave bears were much like modern brown and black bears in this regard. The low peak in the youngest age cohort (stage I) may be explained partly by complete ingestion of small cubs by predators or scavengers (Stiner 1998), but the relative frequencies of individuals in cohorts II and III can not be explained away, because the cubs would have been much larger and their bones more robust.

To summarize thus far, information on species representation in the Yarimburgaz fauna and the patterns of bone damage, body part representation, and mortality for the cave bears indicate that most or all of the cave bear remains are causally unrelated to hominid presence at the same site. The bear bone accumulations resulted primarily from nonviolent mortality associated with hibernation over many generations of den use. Attacks on living bears may also have occurred, but this appears to have been uncommon. Canid and hyaenid contact with bear carcasses certainly is indicated by gnawing damage and scatological bone containing bear cub and hare (*Lepus* sp.) remains (see Stiner et al. 1996). Direct contact between cave bears and humans at this site is unlikely.

The faunal and artifactual evidence shows that at least 3 distinct biological agencies contributed to formation of the Middle Pleistocene faunas: hibernating bears, non-ursid carnivores such as wolves, and hominids, in descending importance. The Yarimburgaz faunas represent overlays of many short-term deposition cycles, most of which were unconnected in time. The close spatial associations of diverse biogenic refuse from bears, wolves, hyenas, and humans are best explained by slow or uneven sedimentation inside the cave. Considerably more can be learned about the habits of the Yarimburgaz cave bears from other aspects of their skeletons.

CAVE BEAR DIET: EVIDENCE FROM TOOTH DAMAGE, ADULT SEX RATIO, AND STABLE ISOTOPES

Adult Sex Ratio in Dens and Its Relation to Diet

Hibernation is a bear's strategy for raising exceptionally altricial infants and enduring food scarcity in winter (Ewer 1973; Garshelis and Pelton 1980; Rogers 1981, 1987; Tassi 1983; McNamee 1984; Murie 1985; Clevenger et al. 1992). In modern bears, the importance of hibernation to both sexes increases with the population's dependence on seasonal foods. And the probability of either sex dying in dens is partly a function of time spent in these places.

Mother bears must hibernate for several months before cubs are mobile (Johnson and Pelton 1980). In contrast, adult males and barren females need only hibernate as long as food is unavailable (Johnson and Pelton 1980, Rogers 1987:20–24, Schwartz et al. 1987, Hellgren et al. 1990:291, Miller 1990, Van Daele et al. 1990, Smith et al. 1994, Weaver and Pelton 1994). One key to adult brown bear sex ratios in dens appears to be winter meat from large game (Picton and Knight 1986) available dur-

ing the months when bears can not find foliage, plant mast, tubers, invertebrates, and most small vertebrates. The degree to which adults other than pregnant females depend on seasonally available foods therefore affects the adult sex ratio of the hibernating population. Males of a relatively herbivorous population should have hibernation times approaching those of pregnant females, less if reliable food sources can be found in winter.

The adult sex ratio of a bear population also is subject to considerable imbalance independent of who hibernates and who does not, often favoring adult females (Craighead et al. 1974, Rogers 1987). This means that the standard against which bear sex ratios in dens are evaluated must be tempered by a consideration of the sex structure of the total adult population from which the death assemblage derives. The adult sex structure of ancient cave bear populations can not be known absolutely, but it can be inferred in relative terms from indirect evidence. Bear sex ratios in the population at large tend to be even at birth (Rogers 1987, Kolenosky 1990, Miller 1994), but sex ratios normally are skewed in favor of females in adulthood (for black bears, Rogers [1987] reports M:F 1:2; for brown bears, Smith [1990] reports M:F 1:3; Clarkson and Liepins [1994] M:F 1:2).

Because black bears are highly omnivorous and may hibernate for up to 7 months (Kolenosky and Strathearn 1987, Schwartz et al. 1987, Miller 1990, Smith et al. 1994)—among the longest hibernation times for bears (Miller 1990)—a similar sex ratio in a paleontological population of any bear species would imply a heavy dependence on plant and invertebrate foods. A greater dietary emphasis on large mammals (scavenged or hunted) or Pleistocene habitats characterized by mild winters instead should result in substantially greater differences between pregnant female and adult male hibernation times (Kolenosky and Strathearn 1987, Miller 1990, Van Daele et al. 1990, Weaver and Pelton 1994), and, consequently, the overall probabilities that the bones of each sex will become part of fossil assemblages in caves. Modern polar bears, which are fully carnivorous and live in very cold regions, represent the opposite extreme which proves the rule: adult males may not hibernate at all and therefore would seldom if ever die inside ice dens (M/F 0:100).

Using an adaptation of Gordon and Morejohn's (1975) metric technique, the sex ratio of the adult cave bears from Yarimburgaz Cave is estimated to have been 73 males for every 100 females (Stiner et al. 1998). All juvenile individuals were eliminated from this comparison because the naturally even sex ratio at birth in bears is bound to push the total population pattern toward evenness, independent of that population's foraging habits. The sex ratio of cave bear samples from Europe varies

between 30:100 to 100:100 males to females, but there is a tendency toward evenness in adult sex ratios overall (summarized in Kurtén 1976:76–77). The sex ratio of the Yarimburgaz cave bears from Turkey therefore is consistent with the pattern found for the European cave bear samples.

It is interesting that the sex ratio of adult cave bears lies at one extreme of the full range of possible patterns in *Ursus*. The mild female bias in the Yarimburgaz cave bears falls well beyond the range typical of modern bears in general and may best resemble that of highly omnivorous black bears. The sex ratio of the cave bears suggests 2 important things about them: (1) the living population was not poor in adult males in Turkey or elsewhere; and (2) these animals depended very heavily upon seasonal food resources. The sex ratio specifically contradicts the possibility of a regular, heavy emphasis on large game. Whether cave bears were firmly at the vegetarian end of the dietary continuum in every region where their remains are found is unclear, but a dedication to highly seasonal food sources is indicated by the adult sex ratio, dental morphology, and damage to the teeth (below).

Tooth Damage and Feeding Habits

The cave bear's dental specializations include cheek teeth with many cusps, large occlusal surfaces in relation to crown height, and a cranial architecture mechanically suited to grinding and crushing (Kurtén 1976:18, Baryshnikov 1998). The extent of occlusal wear in cave bear molars is exceptional relative to that seen in brown bears: molar crowns were often completely obliterated in old cave bears across the many regions where they have been studied. Among elderly cave bears from Yarimburgaz, several first and second molars were worn to stubs and the pulp cavities fully exposed prior to death. The damage to cave bear cheek teeth corroborates routine consumption of tough plant materials such as nuts, hard-coated seeds, tubers and other roots, berries, foliage, and the like. Mattson (1998) reached a similar conclusion about cave bear feeding habits based on interspecific morphometric comparisons of modern and Pleistocene bear crania (i.e., a heavy emphasis on root grubbing).

Koby (1940, 1953) noted peculiar wear and breakage patterns on the anterior teeth of some European cave bears. Many of the Yarimburgaz cave bear canines likewise were broken or chipped during life and worn through continued use. These and other anterior teeth were also seriously damaged by interstitial wear and abrasive forage. Of the ageable adult canines that had come into wear by the time of death, 31% had been broken in some way. Some modern brown bear populations also display

peculiar wear on and frequent breakage of the canines (A. Clewenger, Banff National Park, Alberta, Canada, personal communication, 1995).

The frequency of adult canine breakage is very high relative to that observed by Van Valkenburgh and Hertel (1993) for modern and Late Pleistocene carnivores of North America, where this phenomenon was related to bone feeding and feeding competition. The relative incidence of canine breakage in the Yarimburgaz cave bear sample is amplified somewhat by the advanced ages of the adults therein, but this bias does not wholly account for the high frequency of damaged canines. The biomechanical argument of frequent asymmetrical loading on the canine teeth (Van Valkenburgh and Hertel 1993) probably also applies to the Eurasian cave bears, but the dietary causes of the damage probably do not. The unusually high frequency of damage to the anterior teeth in cave bears is distinctive (B. Van Valkenburgh, University of California, Los Angeles, California, USA, personal communication, 1998) and suggests habitual contact with and levering of hard matter. Intraspecific competition may have added to the damage wrought by feeding. The extreme wear and breakage to the front teeth (canines and incisors) of adult cave bears from Yarimburgaz Cave suggests that food frequently was obtained from cryptic sources requiring actions such as digging and prying (Baryshnikov 1999, Stiner et al. 1998).

Isotope Signals in Bear Tooth Enamel

Quade, Pigati, and Achyuthan of the University of Arizona examined the carbon and oxygen isotopic composition of the enamel of cave and brown bear teeth from Yarimburgaz Cave (Stiner et al. 1998) to address questions about dietary preferences, such as between marine and terrestrial sources, and whether the signals obtained from cave and brown bear teeth differ. Tooth enamel was preferred over other skeletal materials for this study on grounds that its dense, coarsely crystalline structure tends to preserve an original paleodietary signal better than do the less dense mineral structures of bone and dentin (Lee-Thorp and van der Merwe 1987, Lee-Thorp et al. 1989, Thackeray et al. 1990, Quade et al. 1992).

Twenty-three teeth were analyzed, 21 from cave bears and 2 from brown bears. The carbon analyses yielded a mean $\delta^{13}\text{C}$ value of $-15.1 \pm 0.7\text{‰}$ and a range of -14.1 to -16.4 . The results from the brown bears, although from only 2 teeth, were essentially indistinguishable from those for the cave bears. The oxygen analyses indicated an average value of $-6.5 \pm 1.0\text{‰}$ in $\delta^{18}\text{O}$ and a range of -4.9 to -9.0 . The fossil bear teeth from Yarimburgaz Cave retained an unaltered carbon isotopic composition very

similar to that of modern herbivores and carnivores living in regions dominated by C_3 vegetation, such as around the Mediterranean Sea today. Marine resources were not an important component of the diets of the Yarimburgaz bears, even though Yarimburgaz Cave was situated in a near-coastal setting during the Middle Pleistocene.

The carbon isotope results for the Yarimburgaz bears closely match measurements from some cave bear samples in western Europe (Bocherens et al. 1994, Hilderbrand et al. 1996). Bocherens et al. (1994) obtained $\delta^{13}\text{C}$ values on cave bear apatite of $-14.8 \pm 0.7\text{‰}$ ($n = 15$), remarkably close to those of the Yarimburgaz bears at $-15.1 \pm 0.6\text{‰}$ ($n = 21$). Such concordance suggests that the dependence of cave bears on terrestrial food sources was geographically widespread. However, Bocherens et al. (1994) and Hilderbrand et al. (1996) disagreed on the extent of herbivory in cave bears as evidenced by nitrogen isotope measurements. Our isotope results cannot speak directly to this issue, as carbon isotopic values are not good discriminators of trophic level and the protein sources of nitrogen probably are not preserved in the Yarimburgaz specimens due to their great antiquity. Other sources of information on the Yarimburgaz cave bears do speak to this issue: adult sex ratios in dens and dental evidence contradict a high degree of carnivory in the Middle Pleistocene sample from Turkey as well as for other fossil cave bear populations.

SEXUAL SIZE DIMORPHISM IN CAVE BEARS

Modern bears exhibit comparatively high levels of size dimorphism between the sexes. Grossly analogous differences in adult stature and weight have been inferred for Pleistocene *Ursus* species of the northern hemisphere based on the dimensions of canine teeth and weight-bearing limb bones (e.g. Koby 1949; Kurtén 1958, 1976). The results on the Yarimburgaz cave bears (Stiner et al. 1998) are based on measurements of carpal or wrist bones (pisiform and scapholunate; Stiner et al. 1998), using Josephson et al.'s (1996) method-of-moments (MoM) technique. This technique assumes that the total distribution of a metric trait is composed of 2 underlying normal distributions, one for males and one for females. Three moments around the mean of the combined-sex distribution are used to estimate the means and the common standard deviation of the 2 underlying distributions. The scale of measurement most easily controlled in paleontological studies is a simple linear one and, to some extent, areal measurements computed therefrom. If the Yarimburgaz size data are extrapolated to yet a third scale of measurement, analogous to body volume or mass, adult male cave bears would have been roughly twice the lean

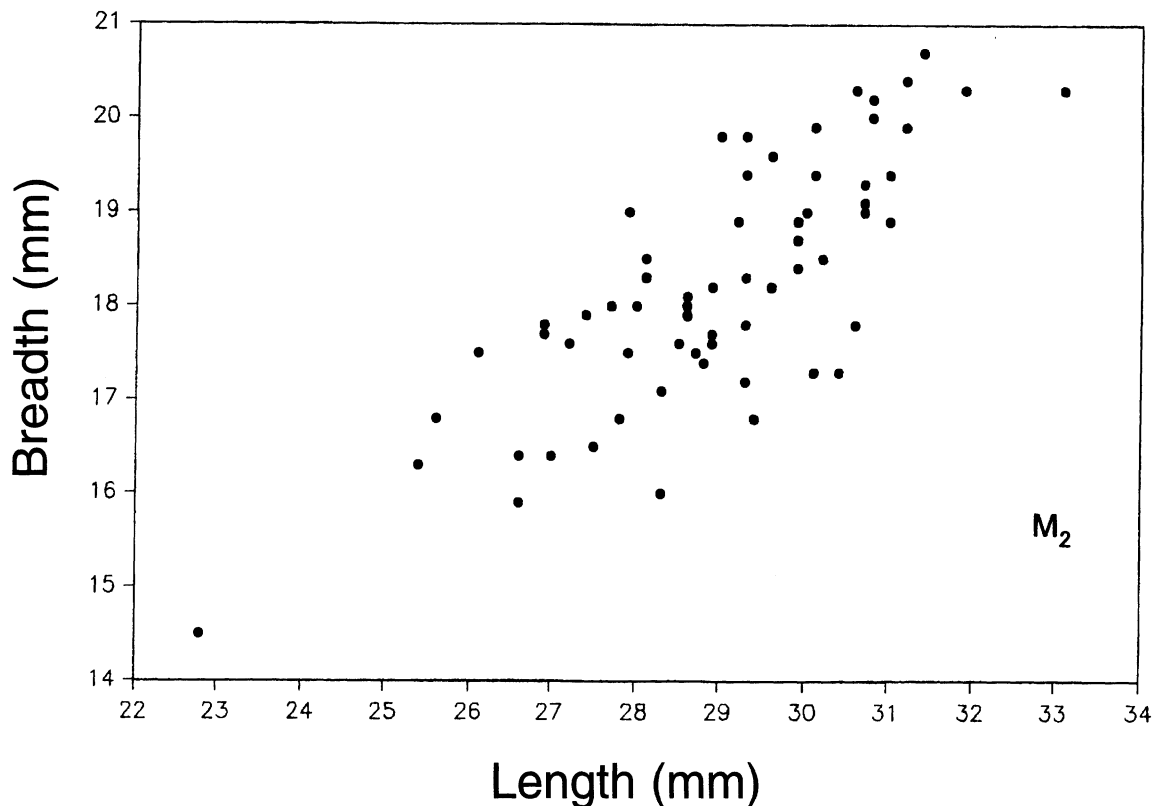


Fig. 5. Scatter plot of length (L) and breadth (B) measurements for right and left mandibular second molars (M_2) of bears from the Middle Pleistocene layer of Yarimburgaz Cave. The isolated point near the graph intercept is a brown bear molar ($n = 1$) >3 SD smaller in both dimensions than cave bear teeth ($n = 64$). Male and female teeth are continuously distributed.

body weight of adult females. This level of sexual size dimorphism is relatively extreme among terrestrial mammals, but not unusual among large-bodied populations of modern brown bears. We infer from this that their mating system was similar to that of extant *Ursus* species.

HOW DID COEXTANT CAVE AND BROWN BEARS DIFFER?

Osteometric techniques demonstrate the presence of 2 Middle Pleistocene bear species in the Middle Pleistocene deposits of Yarimburgaz Cave—*Ursus (Spelearctos) deningeri*, a large cave bear, and *U. arctos* or brown bear—the former abundant and the latter rare. Acknowledging potential time-averaging effects on fossil assemblages, it nonetheless seems that cave and brown bears coexisted in many areas of Eurasia. Cave bears may have been more prevalent in some regions and periods, possibly at the expense of brown bears, and vice versa.

Brown bear teeth from Yarimburgaz Cave are easily distinguished from cave bear teeth on the basis of size. The only brown bear tooth in the M_2 sample, for example

(Fig. 5), falls well below the maximum (mean) proportional size difference that can be expected between the sexes in any terrestrial mammal (roughly males/females = 1.45–1.50 by a linear standard), even in highly size dimorphic lineages such as bears or the great apes (Pongidae). The other 64 data points form a single cluster (Fig. 5), representing a continuous distribution of male and female cave bear tooth measurements. In addition, an informal comparison of the fifth metacarpals of a mature cave bear and a mature brown bear from Yarimburgaz Cave (Fig. 6) exemplifies dramatic structural differences between the 2 species. The brown bear metacarpal is only somewhat shorter than that of the cave bear, but the difference in robusticity is great.

The limb allometry of cave and brown bears also differed. Cave bears possess relatively shorter distal limb elements and longer upper elements than is typical in brown bears (Kurtén 1976, Mattson 1998). The cave bear build is interpreted to have emphasized strength over agility or a quick gate, whereas brown bears are relatively fast runners over short distances. Tooth morphology testifies further to differences among brown and cave bears, not least of which were the extraordinary milling



Fig. 6. Gracile and robust bear fifth metacarpals corroborating the presence of 2 bear species (*U. deningeri* and *U. arctos*) in the Yarimburgaz Cave deposits (Stiner et al. 1998).

capabilities evidenced in the latter. The hyper-developed dental architecture of the cave bear is arguably among the most telling feature in its ecology, as it is expressed by highly conservative elements in the evolution of mammalian skeletons—molar and premolar teeth.

The evolutionary effects of limiting similarity are expressed in the bone and dental structures of cave and brown bears. It is interesting in light of this that we cannot distinguish the diets of coextant cave and brown bears in the Yarimburgaz sample on the basis of carbon and oxygen isotope analyses. The isotope data do yield some insights on the diets of cave bears, but these approaches may lack much of the resolution required to differentiate between coextant cave and brown bear diets; perhaps many of the dietary differences exist *within* the food categories compared by isotope studies (e.g., among C_3 plants). In addition to anatomical differences, cave bear hibernation sites tend to be concentrated at relatively high altitudes, thus accounting for their high density in the modern countries of Switzerland and Austria (Rabeder and Nadel In Press). Cave bears were not confined to highlands—their remains also occur in caves at sea level in low frequencies (e.g. Stiner 1994)—but brown bear remains seem to be more common at lower altitudes, as are human archaeological sites dating to before the Upper Paleolithic period.

DISCUSSION

Cave bears inhabited a vast area stretching from western Europe to the Urals, Siberia, and into west and cen-

tral Asia; their Pleistocene distribution was considerably greater than was previously supposed (Kurtén 1976; Baryshnikov 1989, 1996, 1998; Tchernov and Tsoukala 1997; Stiner et al. 1998). Cave bears coexisted with brown bears and early humans throughout most or all of this range during the Middle and Late Pleistocene. The classic cave bear form appears in the fossil record roughly 700,000 years ago and persists in many areas until the Last Glacial Maximum, 18,000 years ago, and until the end of the Pleistocene (10,000 years ago) in refugia of the Trans-Caucasian highlands (Baryshnikov 1996). Only the brown bear exists in these and other regions today. With its eventual colonization of American ecosystems, the once exclusively Eurasian brown bear enjoys the widest distribution known for any bear species in the late historic period (Kurtén 1971).

Cave and brown bears have a long history of contact with humans, but evidence for direct interaction is relatively rare. Of these cases, most of the compelling examples of direct interaction are between humans and brown bears. Images of bears are featured in the earliest art of Europe, beginning some 32,000 years ago in the Upper Paleolithic. Kurtén's (1976:91) claim that brown bears were more often the subject of early art continues to hold true, even with the recent discovery of the carnivore-rich imagery in Chauvet Cave (Chauvet et al. 1996). The relatively few images of cave bears that exist in Upper Paleolithic cave art—such as in the French sites of La Colombière, Les Combarelles, and Chauvet—portray an animal with an enlarged shoulder hump, accentuated stop in the nasal bridge, and relatively fleshy nose and lips. Upper Paleolithic art is not without its fanciful elements, but some aspects of these paintings may be quite accurate.

But what about early cases of bear-artifact associations, dating to before the dawn of Upper Paleolithic cultures and the earliest preserved art? Taphonomic investigations of Yarimburgaz Cave and other sites refute the possibility of causal links between cave bear and hominid occupations (Prat 1988, Andrews and Turner 1992, Gargett 1996). The close proximity of bear bones, stone artifacts, ungulate, and non-ursid bones in the Middle Pleistocene layer of Yarimburgaz Cave reflects contemporaneity only on a geologic time scale, not at the scale of mammalian lifetimes or annual cycles. Preserved records of these events were superimposed, one directly upon another, because the rate of sediment accumulation was slow relative to the rate of bone and artifact accumulation and because of post-depositional disturbances by bedding bears and other digging carnivores. Human occupations of the early sites were quite ephemeral, short visits separated by long intervals of

absence. Under these circumstances, early humans would have provided few if any deterrents to den-seeking bears. Despite its long history of use by numerous large mammals, it seems that Yarimburgaz Cave was often an empty, quiet place.

The case of Yarimburgaz is one of several windows on cave bear ecology, as well as early humans' relations with them. The findings presented here confirm a picture of cave bears as a relatively herbivorous omnivore, highly dependent on seasonal food supplies, including plants, and probably also invertebrates and small vertebrates. Both sexes of cave bears solved the problem of winter food scarcity by hibernating. Male and female cave bears were as size dimorphic as large-bodied populations of modern brown bears, suggesting similar mating systems, specifically the degree of male-male competition for mates. Cave bears were perhaps most different from other bears in their ability to extract nutrients from tough, resistant, and often gritty plant tissues. In so doing, old adults frequently wore their massive molars to pegs, a condition not unknown in brown bears, but certainly not as typical nor as widespread among populations. Although more work is needed on the subject, cave bears appear to have been terrestrially oriented, even in territories adjacent to productive seas (Hilderbrand et al. 1996).

As for cave bears' ecological relations with early humans, we have had to deal first with how archaeological and paleontological records form and the possibility that separate biogenic events were recorded surficially as one. Knowledge of how modern bears behave and die makes Paleolithic artifact-bear associations difficult to understand if taken at face value. Only a cross-disciplinary perspective, informed by wildlife data on modern animal behavior and by the nature of sedimentary processes, allows us to explain this phenomenon. The possibility of a cave bear cult among the Neandertals has been falsified, and in its place is a more interesting story of coexistence between omnivorous lineages whose resource interests occasionally overlapped.

As omnivores, humans' and bears' options for switching among alternative food sources have always been considerable. While it is possible that humans eventually drove cave bears to extinction, this is not at all certain. It is not clear, for example, that cave bears competed directly with humans for food, even if they may have competed with humans for territory. Human population densities were very low during most of the Middle Paleolithic and earlier (Stiner et al. 1999). Human densities increased during the Upper Paleolithic period, especially following the Last Glacial Maximum (18,000–20,000 years ago), when cave bears were disappearing from most

areas except certain highland refugia. It is interesting that the earliest grinding and pounding technology emerges in Upper Paleolithic cultures, Lilliputian implements geared first to preparing mineral pigments but later enlarged and adapted to processing nuts (and eventually cereals) in some regions by 13–10,000 years ago. Late Upper Paleolithic humans may merely have expanded their foraging niche as it was released from competition by large-molared cave bears, or as favorable plant communities expanded with climate change.

The intensity of human occupations in natural shelters, which also increased after 18,000 years ago (Gamble 1986), may have affected these shelters' attractiveness and availability to den-seeking bears. We do not know, however, if, perhaps owing to their great body size, cave bears depended more on caves as denning sites than brown bears. We only know that bones preserve better in caves than in the open. The necessary links between caves, cave men, and cave bears are largely of a geological nature and say little or nothing about the possibility of habitation and den sites elsewhere on landscapes.

More significant than the possibility of interspecific competition between early humans and cave bears is the peculiar nature of cave bear skeletal structure. Cave bears were a specialized, highly derived type of bear, arising from a larger lineage which otherwise emphasized generalized characters. The fact that cave bears specialized under predominantly glacial conditions (most of the Pleistocene) itself may provide a more compelling explanation for their extinction at the beginning of the modern interglacial (Holocene). The dentition of cave bears is exceptional for a bear. Specialists are particularly vulnerable to extinction when the conditions of life become unstable, and those following the Last Glacial Maximum, a rapid process of global warming, were among the most trying for large Pleistocene mammals. Whatever effect these factors had on cave bears, they did not affect brown bears in the same way. Brown bears have retained many generalist features and habits, and this flexibility no doubt aided their great success in weathering the Holocene transition.

Wildlife data, such as that on modern bears, are important referents for zooarchaeological research on the evolutionary history of human beings as well as on the species with whom they may have interacted. Archaeologists do not have the luxury of directly observing the phenomena that drive our discipline. Through a series of inferential steps, we extract information from coarse, imperfect behavioral and morphological records. The efficacy with which we do so depends on clear expectations about the relations among key variables, many developed in the contemporary world, but which also find

expression in fossil animal assemblages. The present frequently informs research on past. Insights about modern conservation issues may also be gained from the long view of humans' relations with coextant species.

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