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# Cave Bears from Southern Germany: Sex Ratios and Age Structure. A Contribution Towards a Better Understanding of the Palaeobiology of *Ursus spelaeus*

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ABSTRACT: Sex ratios of cave bears (*Ursus spelaeus* and *U. deningeri*) are known to vary greatly between sites. A number of explanations have been proposed to account for this variability, involving for example cave size, altitude, and the seasonality of food availability. This contribution presents demographic data from three sites in southern Germany which allow the rejection of these models; the factor(s) behind the variability in sex ratios is (are) still unknown. The data also suggest that, contrary to the case in living brown bears (*U. arctos*), males in cave bears may have reached a very old age more frequently than females.

KEYWORDS: CAVE BEAR, SEX RATIOS, AGEING, DEMOGRAPHY, SEXUAL DIMORPHISM

RESUMEN: La proporción de machos y hembras de osos de las cavernas (*Ursus spelaeus* y *U. deningeri*) varía de gran manera entre diferentes localidades. Algunos modelos, que incluyen factores como el tamaño y la altura sobre el nivel del mar de las cuevas, así como la estacionalidad de los alimentos disponibles, han sido propuestos para explicar esta variación. Sin embargo, datos demográficos de tres sitios en el sur de Alemania, expuestos en el presente artículo, permiten el rechazo de estas hipótesis. Los factores que contribuyeron en la determinación de las proporciones de ambos sexos son todavía desconocidos. Los datos sugieren también que, a diferencia de lo que ocurre en el oso pardo actual (*U. arctos*), los machos de *U. spelaeus* alcanzaban una edad muy avanzada más frecuentemente que las hembras.

PALABRAS CLAVE: OSO DE LAS CAVERNAS, PROPORCIÓN DE SEXOS, EDAD, DEMOGRAFÍA, DIMORFISMO SEXUAL

## INTRODUCTION

The Late Pleistocene cave bear (*U. spelaeus*) is among the most common and most intensively studied of all fossil mammals. The vast numbers of its remains in European caves have enabled scholars to obtain a fairly complete picture of its geographical distribution, anatomy, evolution, and pathology (e.g., Fraas, 1862; Abel, 1931; Breuer, 1931; Ehrenberg, 1931, 1935; Koby, 1949; Kurtén, 1955a, 1955b, 1957, 1959, 1976; Musil, 1965; Cuggiani, 1981; Rabeder, 1983, 1991, 1999; Torres Pérez-Hidalgo *et al.*, 1991; Groiss, 1994; Grandal-D'Anglade & Vidal Romaní, 1997). Nevertheless, in spite of the wealth of its remains, many important aspects of its palaeobiology remain poorly understood. Which factors delimited the geographical distribution of the cave bear? Why did this species, in contrast to its cousin the brown bear (*U. arctos*), go extinct at the end of the Pleistocene? Even the long-held belief that *U. spelaeus* was exclusively vegetarian must now be apparently questioned (Hildebrand *et al.*, 1996; but see Bocherens *et al.*, 1994 and Fernández Mosquera, 1998).

The fact that *U. arctos* survived the last glacial whereas *U. spelaeus* did not, points to the existence of important differences in the palaeobiology and palaeoecology of these two species. Thus, while for some purposes some physiological characteristics of the brown bear can (or, lacking any alternatives, rather *must*) be considered an approximate guide for the cave bear, e.g., concerning timing of tooth eruption and time of birth, many aspects from their palaeobiology must be deduced from the fossil record itself.

Among the most important characteristics of any mammal population is its demographic structure, since it is determined by both the reproductive biology of the species in question as well as by the interaction of the population with its environment (Kurtén, 1964). Thus, demographic parameters gained from fossil and sub-fossil assemblages, such as age structure and adult sex ratio, can be of considerable importance for the understanding of the palaeobiology and palaeoecology of extinct species.

Many reports on cave bear assemblages describe the demographic characteristics at the site (e.g., Ehrenberg, 1931; Kurtén, 1958; Musil, 1965; Rabeder, 1991; Andrews & Turner, 1992; Grandal-D'Anglade & Vidal Romaní, 1997; Stiner, 1998; Stiner *et al.*, 1998). The interpretation of the age structure in the different sites is often straightforward and convincing (e.g., Kurtén, 1958; Andrews & Turner, 1992; Stiner, 1998). In most cases, juveniles and older adults form the largest part of the assemblages. This can be considered as a clear indication that most individuals died during hibernation (Kurtén, 1958, 1976; Stiner, 1998; Stiner *et al.*, 1998). In contrast, with a few exceptions, sex ratios are only described but not further interpreted. Sex ratios of adult cave bear vary greatly between sites or sometimes even between layers in a single site (Table 1 & Figure 1). At many sites, the sex ratio is approximately even or shows a slight dominance of females (e.g., Yarimburgaz, Odessa, Cotencher, and Dachstein). At others sites, e.g., Saint Brais, Cueva del Toll, Ekain, females clearly outnumber males, whereas males are much more abundant at Arrikrutz and in the upper levels of Mixnitz. In fact the observed variability in the sex ratios is so large that the few interpretations of sex ratios which have been made, usually based in one or a couple of sites, break down when applied to localities other than the ones for which the model was proposed (see below). In other words, if we are to understand this aspect of cave bear palaeobiology, what is needed is an explanation of the *variability* of the sex ratios between different sites rather than different models for each bone assemblage.

This paper should be seen as a contribution towards the understanding of the variability of sex ratios in cave bear. Here, the cave bear remains of three south German sites are investigated: the Bärenhöhle-Hohlenstein and the Sibyllenhöhle in the Swabian Alb and the Zoolithenhöhle in the Frankonian Alb (Figures 2 & 3). The collections from the Bärenhöhle and the Sibyllenhöhle are stored at the State Museum of Natural History in Stuttgart (SMNS). These two caves were excavated in the second half of the 19th century and much of the their fossil material has been subsequently lost. In fact, it has been argued that, due to the selective preservation of the material, adult sex ratios of *U. spelaeus* in these assemblages are so biased as to be completely useless (Adam, quoted in Kurtén, 1976). It can be shown, however, that the sex ratios at these sites are not as distorted by post-excavation factors as Adam suggested; this point is discussed in full in the Appendix.

## EXPLAINING THE VARIABILITY OF SEX RATIOS

Since most cave bear assemblages accumulated over a long time span, comprising often thousands of years, it can be discounted that the sex ratios are a product of stochastic processes. Thus palaeobiological/palaeoecological explanations are required.

It must be mentioned that some risk exists that the sex ratios of cave bears in some of the deposits, especially those excavated in the 19th or the first half of the 20th century, in which stratigraphical control is usually poor, may represent an average of changing sex ratios through time. However, due to their recovery methods, these old collections are often quite large, and are thus particularly suitable for biometrical analyses and, consequently, for the calculation of sex ratios. This is a dilemma which cannot be resolved at present; either we use the material we have now and accept the risks involved, or we wait, perhaps for many years, for material with a better stratigraphical control to become available. I have opted for the former.

| site | country | sex ratio % (♀:♂) | reference |
|---|---|---|---|
| Arrikrutz | Spain | 21 : 79 | Torres Perez-Hidalgo et al., 1991 |
| Conturines | Italy | 84 : 16 | Reisinger & Hohenegger, 1998 |
| Cueva del Toll | Spain | 80 : 20 | Torres Perez-Hidalgo et al., 1991 |
| Drachenloch | Switzerland | 65 : 35 | Jequier, 1975 |
| Einhornhöhle | Germany | 75 : 25 | Schütt, 1968 |
| Eirós* | Spain | 58 : 42 | Grandal D'Anglade & Vidal Romaní, 1997 |
| Ekain | Spain | 71 : 29 | Torres Perez-Hidalgo et al., 1991 |
| Hastière | Belgium | 40 : 60 | Ehrenberg, 1935 |
| Mixnitz, up. levels | Austria | ~ 30 : 70 | Bachofen-Echt, 1931; Ehrenberg, 1931 |
| Mixnitz, low. levels | Austria | ~ 50 : 50 | Bachofen-Echt, 1931; Ehrenberg,1931 |
| Odessa | Ukraine | 53 : 47 | Kurtén, 1955a |
| Pod hradem 15 | Czech R. | 42 : 58 | Musil, 1965 |
| Pod hradem 12 | Czech R. | 75 : 25 | Musil, 1965 |
| Sima de los huesos+ | Spain | ~ 77 : 23 | García et al., 1997 |
| Troskaeta | Spain | 60 : 40 | Torres Perez-Hidalgo et al., 1991 |
| Trou de Sureau | Belgium | 47 : 63 | Ehrenberg, 1935 |
| Westbury+ | G. Britain | 75 : 25 | Bishop, 1982 |
| Wildkirchli | Switzerland | 46 : 54 | Jequier, 1975 |
| Yarimburgaz+ | Turkey | 58 : 42 | Stiner, 1998 |

* means of sex ratios from a number of skeletal elements; + *Ursus deningeri*

TABLE 1

Sex ratios of cave bears in some Eurasian sites.

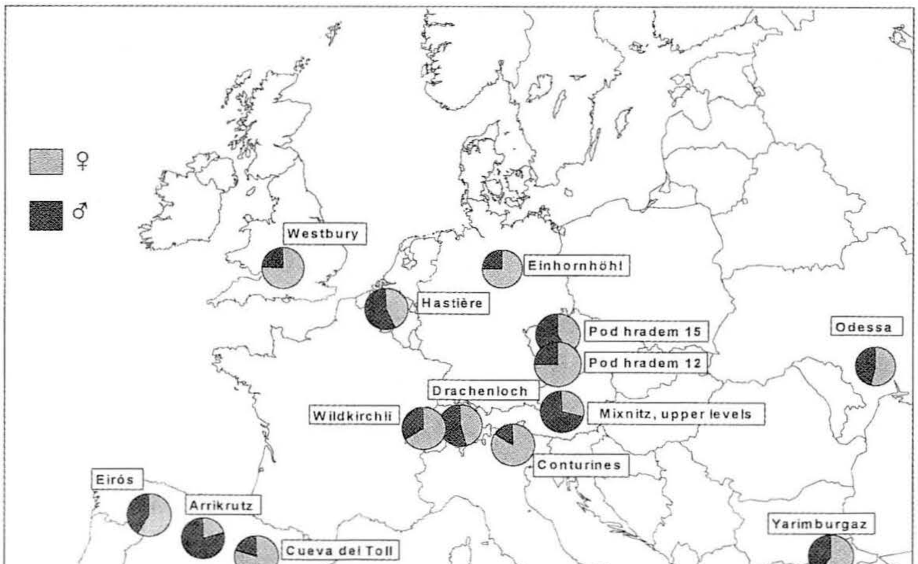

FIGURE 1

Sex ratios in some cave bear assemblages (for data sources see Table 1).

A further complication in the interpretation of sex ratios of cave bear is the lack of data on the demography of those individuals dying in the open; would their sex ratio be complementary to the one observed in the caves in the vicinity? Again, this question must be ignored for the time being but the investigation of the season of death of the few cave bears found in open air sites, e.g. through cementum increment analysis, would certainly help to clarify the issue.

Abel (1929, 1931) arguing from the evidence of the Austrian site of Mixnitz, saw in the clear overrepresentation of males in the upper levels evidence supporting his theory of a degeneration of the cave bear during the Last Glacial culminating in its extinction: a change in the heredity of the species led to a differential birth-rate producing a superabundance of males relative to females. Kurtén (1976) refuted this hypothesis by showing that the sex ratio in Mixnitz was male-biased for the adults only; among the juveniles it was approximately 1:1. Abel's model can also be easily dismissed by the fact that other caves dating like Mixnitz to the later part of the Upper Pleistocene, such as Odessa (Kurtén, 1969), have a female-dominated sex ratio.

Kurtén (1958, 1976) considers an active choice by the bears themselves as the explanation for the variability in the sex ratios. Male brown bears are known to kill and eat cubs and Kurtén assumes that this was the case for cave bears as well. Thus, in order to protect their young, pregnant females or those with cubs would seek small, easily surveyed and defendable shelters where they and their progeny would hibernate. Males, in contrast, were less selective and hibernated also in large caves, even if already occupied by other individuals. According to Kurtén (1958, 1976) it is no coincidence that in the small cave of Saint Brais in Switzerland females outnumber males by as much as 3:1 while in the huge cave of Mixnitz males are more abundant.

FIGURE 2
Location of investigated sites in southern Germany.

A different explanation for the variability of sex ratios was proposed by Reisinger & Hohenegger (1998) in a recent paper on cave bears from three sites in the Eastern Alps. Here, a correlation was suggested between the proportion of females and the altitude of the caves. The authors suggest that female-biased sex ratios in caves in "ecologically extreme areas" (e.g., higher altitudes) are probably a result of the need of females to protect their cubs from male intruders. In the Conturines in northern Italy, located at an altitude of 2,775 m, the proportion of females ranges, according to the skeletal element analysed, from 72%-84%, whereas females in the lower situated cave of Herdengel (780 m) in lower Austria comprise only 13%-54%. In Gamssulzen, intermediate in altitude between the two sites mentioned above (1,300 m), the sex ratio varies from 43%-87% (the differences in sex ratios between different skeletal elements is probably a product of the relatively small sample size; If only the most abundant element at each site is taken into account, the proportion of females are as follows: Conturines 73%, Gamssulzen 84%, and Herdengel 13%).

Yet another explanation of the variability in sex ratios of cave bear was postulated by Stiner *et al.* (1998) in a paper about Middle-Pleistocene cave bears (*U. deningeri*, regarded as *direct* ancestor of *U. spelaeus*) from Yarimburgaz cave in Turkey. It is suggested that the adult sex ratio may be a reflection of the diet of the population in question. In modern bear populations, all pregnant females must hibernate for several months in order to allow the cubs, born during hibernation, to develop. Males and barren females, in contrast, must not hibernate as long as food is available in winter (Stiner *et al.* 1998). The more scarce the food in winter is, the more

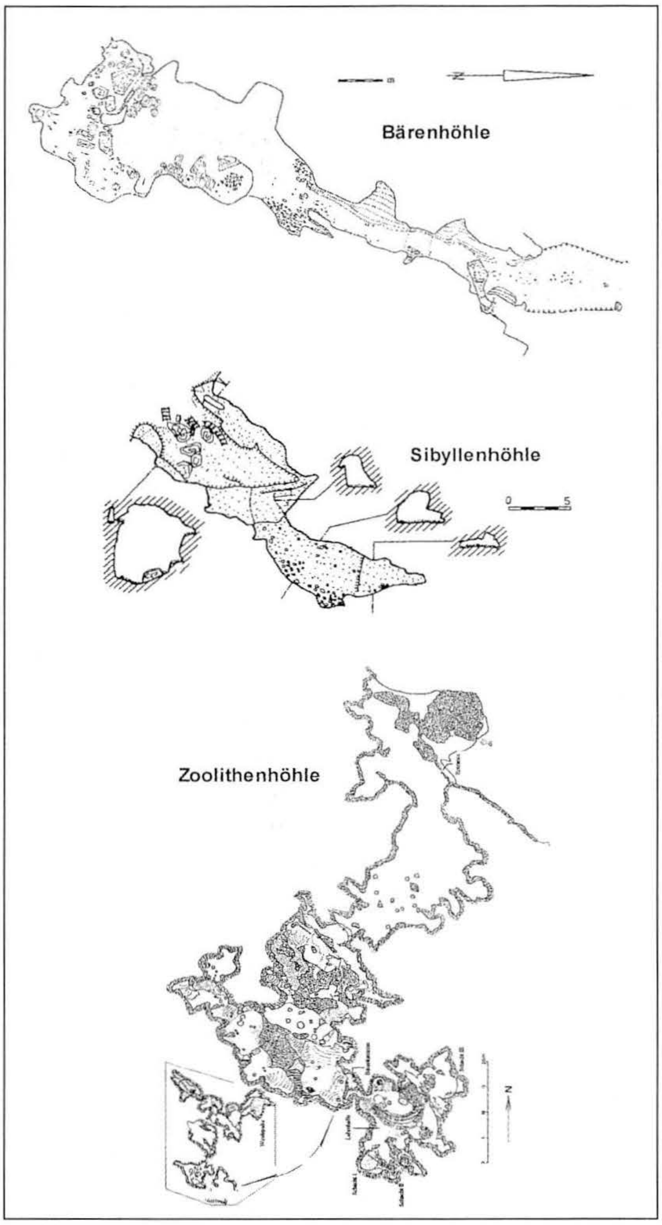

FIGURE 3

Maps of Bärenhöhle (after Schmid, 1989), Sibyllenhöhle (after Bronner, 1979), and Zoolithenhöhle (after Niggemeyer & Schubert, 1972).

males would hibernate, and also die during hibernation within the cave. Thus the sex ratio becomes more even as the food supply becomes more seasonal. From the sex ratio in Yarimburgaz, only slightly skewed towards the females, Stiner *et al.* (1998) deduced that the bear population in this area depended heavily upon highly seasonal resources.

As it will be discussed below, the present investigation of the *U. spelaeus* assemblages from southern Germany allow us to reject at least some of these models.

## MATERIAL

### *The Bärenhöhle*

First excavated by O. Fraas in 1861, this cave is located in the limestone cliff outcrop known as the Hohlenstein, on the right bank of the Lone valley (467 m a.s.l.). It consists of a narrow passage, some 1-1.5 m in height and 35 m in length, extending in a N-S direction and giving way to a spacious chamber, which Fraas subdivided into three different chambers, up to 10 m high and some 15 m in diameter (Fraas, 1862; Figure 3).

About 10,000 bones were recovered from the site (Fraas, 1862), from which 98% belonged to *U. spelaeus*. From this amount, 7,000 were considered worth taking back to the Museum in Stuttgart, while the rest was left at the site. During the following years large quantities of material were given away to museums and institutions in Germany and elsewhere, so that today only 3587 fragments are preserved in the collection at the SMNS (see discussion see Appendix).

More recent excavations at the site by Wetzel demonstrated the sporadic occupation of the site by Palaeolithic people during the Mousterian, Aurignacian and Magdalenian (Wetzel, 1961). Thus, the cave bear remains excavated by Fraas, who did not distinguish between layers, span probably some millenia within the last (Würm) glacial. The faunal material from Wetzel's excavations (which was not included in the present investigation) includes *Ursus spelaeus*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus sp.*, *Crocuta crocuta*, and *Cervus elaphus* (Wetzel, 1961).

### *The Sibyllenhöhle*

The cave, near the city of Kirchheim, is situated at the foot of the rock massif known as the Teck (763 m a.s.l.), on top of which a medieval fortress was built. The site was excavated by E. Fraas in 1898 (E. Fraas, 1899). From its spacious entrance in the NW, the cave runs 23 m to the SE, becoming narrower and lower. Its form can be described basically as consisting on a broad and high forechamber and a broad but low rear chamber interconnected by a narrow passage (Figure 3 ).

According to E. Fraas (1899), about 10,000 bone fragments were found, from which most were small splinters with rounded edges. About 2,150 fragments were kept, from which 894 are found today in the SMNS collection (for discussion of material lost see Appendix). As in the Bear Cave, more than 95% of the fragments belonged to *Ursus spelaeus*; other species present include lion *Panthera leo*, hyena *Crocuta crocuta*, and horse *Equus* sp. While it is certain that the fauna dates to the last glacial, a more exact chronological position or the time span represented by the accumulation is unavailable. Traces of human occupation were apparently not found at the site.

### *The Zoolithenhöhle*

Located near Burggaillenreuth (470 m a.s.l.) in the Franconian Alb, Bavaria, this site was explored already in the mid-18th century. In contrast to the Bärenhöhle and the Sibyllenhöhle, the architecture of the Zoolithenhöhle is complicated (Figure 3). The entrance is located in the North; from here, a large chamber extends south for about 40 m. Beyond runs a maze of chambers of irregular form, which are often interconnected through narrow, sometimes vertical passages. The cave owes its name to the word, Zooliths, which Esper (1774) coined to denote the remains of extinct mammals he found in the cave. He realized that the vast majority of the finds belonged to bears. According to Heller (1972), the remains of more than 1000 individuals were recovered at the site. It was with faunal remains from this cave that some years later Rosenmüller & Heinroth (1794) described the holotype *Ursus spelaeus*. From the very abundant faunal material from this early investigation, only a small fraction is known to survive nowadays (Heller, 1972; Groiss, personal communication). During 1971, new excavations in a number of different areas which had not been dug or disturbed previously were carried out (Groiss, 1972). This time, again, considerable quantities of faunal material dating to the last glacial were recovered, consisting mostly of *Ursus spelaeus*, but including also other taxa, notably *Gulo gulo*, *Canis lupus*, *Crocuta crocuta*, and *Panthera leo* (Heller, 1972; Groiss, 1979). Absolute radiometric dates from two different locations within the cave range from ca. 29-24 ka BP (Groiss, pers. comm.).

## METHODS

Among the Ursidae, males are always larger than females. The difference varies, according to species, between 10-20% to 50% (Stirling, 1993). According to Christiansen (1999), large cave bear males weighted about 400-500 kg whereas females reached "only" 225-250 kg. Since the weight must be supported by the extremities, this size difference is apparent in the width and depth of long bones. A clear sexual dimorphism exists also in the canines (Koby, 1949). Thus osteometrical data can be used to establish the relative proportions of both sexes in an assemblage. In this investigation, measurements were taken with a pair of digital callipers to the nearest 0.1mm following the definitions of von den Driesch (1976) and Grandal-d'Anglade (1993). Included in this investigation were all postcranial limb bones showing fused epiphyses; excluded were phalanges, the smaller carpals and tarsals, and sesamoids. Additionally, the first and second cervical vertebrae, and the lower and upper canines were also measured. The biometrical investigation of the material from the Zoolithenhöhle, while in its end stage, has not been completed yet; thus not all skeletal elements from this site have been included.

The distribution of absolute values in some measurements of postcranial elements shows an overlap between males and females; however, bivariate plots can usually separate between the sexes accurately and absolutely, and can thus used to calculate sex ratios. For each one of the three sites dealt with in this paper, sex ratios were calculated from each of the different postcranial elements and the canines, as long as n≥10.

It must be stressed that different skeletal elements can, and often do show somewhat varying sex ratios, not only in bears but in ungulates as well (e.g., Grandal-D'Anglade & Vidal Romaní, 1997; Weinstock, 2000, in press; see below). These variations could sometimes be related to sample size but they are also a result of the fact that different skeletal elements represent somewhat different age classes. For example, the canines in living brown bears erupt at an age of ca. 12 months (Dittrich, 1960) and therefore measured canines will reflect sex ratios of animals 1 year and older. There seems to be no data on the timing of the epiphyseal fusion in brown bear (*U. arctos*), but in the black bear (*U. americanus*) the epiphyses of the bones of the forelimb fuse at an age of 6-8 years (Marks & Erickson, 1966). Thus measured humeri or radii with both epiphyses fused would represent the sex ratio of an age group >6 years. This would not matter much if sex ratios in bear populations remained constant throughout all age classes; however, this is not so. In natural-regulated populations of *U. arctos* the sex ratio at birth is roughly equal; however, there is a preponderance of females in all age classes from sub-adulthood to senescence due to a higher mortality of males, which in turn is a result of males having larger ranges and of their continuing tendency to fight (McNamee, 1997).

In addition to sex ratios, the age structure of the cave bears in each of the three south German caves was analysed. This demographic parameter is relevant for the determination of whether bear mortality occurred mostly during hibernation. Starvation and illness are the main mortality factors during this time, and the corresponding mortality profile is U-shaped, i.e. attritional (Stiner, 1998): young individuals are very well represented, old animals are common, and prime adults rare. In addition to the non-violent mortality factors mentioned above, it is conceivable that hibernating cave bears were also attacked and sometimes killed by conspecifics or other predators such as wolves, hyaenas, lions or humans. If these attacks were frequent, the mortality will resemble more the "living structure" pattern rather than the attritional one, since mortality would affect individuals of all ages equally (Stiner, 1998).

In order to investigate the mortality patterns of the bears of the Bärenhöhle, the Sibyllenhöhle, and the Zoolithenhöhle, a method developed and described by Stiner (1994, 1998) was used. In this method, each tooth is assigned to one of nine different categories or cohorts (I-IX, from young to old) according to its eruption stage and/or its occlusal wear. Stage I, for example, includes all permanent teeth from the germ stage to those with root formation is up to 50% complete. Stage II comprise teeth which are fully (or nearly) erupted, their roots more than 50% complete, but with no visible wear on their occlusal surface. By stage III, some wear of the occlusal enamel is evident but little or no dentine is exposed. At the other extreme, stages VIII and IX include teeth which are very heavily worn, with no or just little enamel remaining in its occlusal surface, and in which the pulp cavities are frequently exposed (Stiner, 1998). These nine cohorts can be pooled into three age stages: juvenile (I-III), prime adult (IV-VII), and old adult (VIII-IX). The relative abundance of specimens in each of the three stages can then be plotted in a ternary (tripolar) graph (Stiner, 1994, 1998). The triangle in this type of graph can be divided into a number of areas, each associated with a mortality pattern family such as the "non-violent attrition" (NNVA) and the "living structure" (LS) patterns (Figure 4).

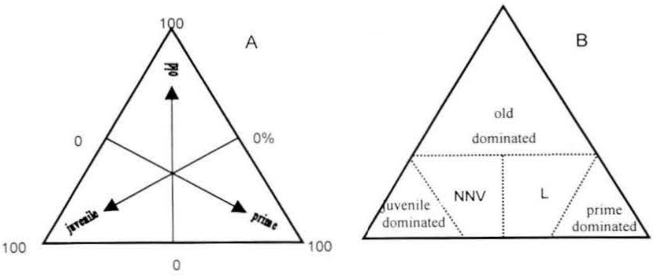

FIGURE 4

Structure of a tripolar age graph (A) and families of mortality patterns (B) (after Stiner, 1990, 1998). The triangle can be divided into different areas, each representing a different mortality pattern. The relative abundance of young, prime adults, and old individuals can throw light on the origins of the thanatocoenose (e.g. death during hibernation, predation, etc.).

In all of the three sites dealt with in this paper mandibles and loose mandibular teeth were much more abundant than maxillaries and maxillar teeth, and therefore the age structure analysis was based only on the former.

Mandibles and loose teeth from individuals in cohorts I and II (i.e. very young animals) are less resistant to mechanical damage than those in older cohorts. Given that the preservation and the recovery methods may differ among sites, the histograms showing the mortality patterns are presented twice in order to facilitate the inter-site comparisons, once including cohorts I and II and once beginning with cohort III.

Stiner's method is definitely an improvement over the traditional four-stage method used frequently (e.g. Musil 1965; Torres Pérez-Hidalgo, 1984; Andrews & Turner, 1992; Grandal D'Anglade, 1993), since it allows a greater resolution, revealing some interesting demographic patterns.

## RESULTS

### *The Bärenhöhle*

The sex ratio of adult bears in this cave, as calculated from bivariate plots, varies somewhat according to the skeletal element examined (Table 2; Figure 5). In all elements, however, males are clearly over-represented; they comprise 63-82% (mean ($\bar{x}$) = 73; median ($\tilde{x}$) = 73). A clear majority of males is uncommon, though not unknown, in cave bear assemblages (e.g., Arrikrutz 79%, Mixnitz upper layers 70%; see Table 1).

| skeletal element | n ♀ | n ♂ | % ♀ |
|---|---|---|---|
| lower canine | 9 | 20 | 31,0 |
| atlas | 7 | 23 | 23,3 |
| axis | 5 | 18 | 21,7 |
| radius | 8 | 15 | 34,8 |
| ulna | 6 | 20 | 23,1 |
| mc II | 7 | 31 | 18,4 |
| mc III | 12 | 33 | 26,7 |
| mc IV | 8 | 34 | 19,0 |
| mc V | 20 | 33 | 37,7 |
| intermedio-radiale | 10 | 19 | 34,5 |
| tibia | 10 | 22 | 31,3 |
| astragalus | 13 | 22 | 37,1 |
| mt II | 6 | 25 | 19,3 |
| mt III | 12 | 30 | 28,6 |
| mt IV | 15 | 57 | 20,8 |

TABLE 2

*U. spelaeus*, number of specimens of male and female and relative abundance of females in the Bärenhöhle.

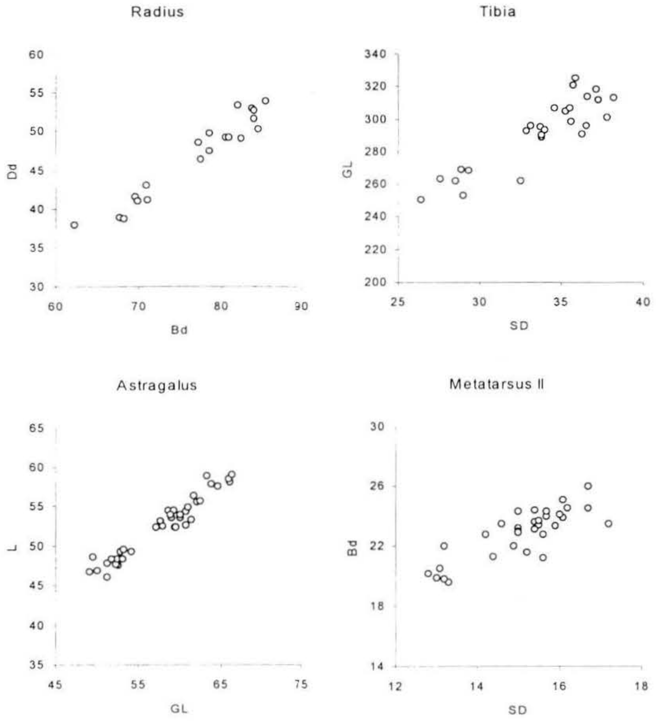

FIGURE 5

*U. spelaeus* from the Bärenhöhle; bivariate plots of a number of skeletal elements. Two groups, representing males and females respectively, are clearly seen in all plots. In all cases the show an overrepresentation of the former.

Tooth wear and eruption indicate that the many bears at this site died at a very young age (Figure 6 & Table 5). All mandibular molars show a very marked peak at cohort I. Most of the mandibles assigned to this category show an unerupted $M_1$. Since this tooth erupts during the fifth month of life (Dittrich, 1960), it can be concluded that these individuals died during their first winter. Juvenile mortality (stages I-III) was 75%. Few individuals (ca. 6.5%) died during their prime age (IV-VII), but old adults (VIII-IX) are more common (15-18%). The U-shaped age structure of the Bärenhöhle death population (Figure 6) indicates a non-violent attritional mortality consistent with death during hibernation (Stiner, 1998).

The simultaneous occurrence of the two demographic characteristics of the bear assemblage in the Bärenhöhle, male-dominated and non-violent attritional (winter) mortality, has important implications for the evaluation of the hypothesized relationship (Stiner, 1998) between sex ratios and seasonality of diet.

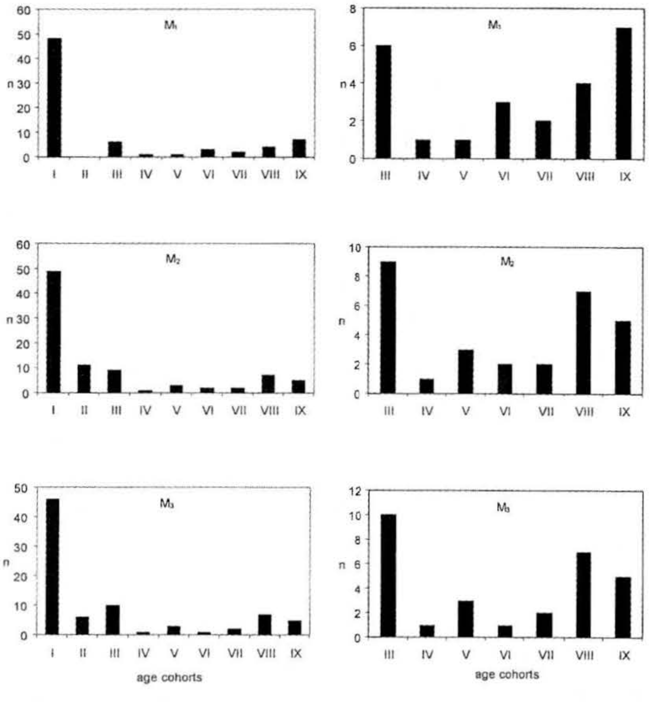

FIGURE 6

Age structure histograms for the Bärenhöhle bear population based on eruption and occlusal wear of mandibular molars. The graphs at the right exclude cohorts I and II, the relative abundance of which could be influenced by taphonomic factors (see text). Neonates (cohort I) dominate in the assemblage; among the older individuals, those in stages III ("young"), and VIII and IX ("old adults") are well represented, while "prime adults" (stages IV-VII) are rare.

| site / age cohort | nr. of specimens determined and percentages of total | | |
|---|---|---|---|
| | $M_1$ | $M_2$ | $M_3$ |
| Bärenhöhle | n= 72 | n= 89 | n= 81 |
| juvenile | 75.0 | 77.5 | 76.5 |
| prime adult | 6.9 | 6.7 | 6.2 |
| old adult | 18.1 | 15.7 | 17.3 |
| Sibyllenhöhle | n=22 | n=16 | n=13 |
| juvenile | 46.2 | 31.3 | 50.0 |
| prime adult | 46.2 | 50.0 | 40.9 |
| old adult | 7.7 | 18.8 | 9.1 |
| Zoolithenhöhle | n= 103 | n= 134 | n= 135 |
| juvenile | 78.9 | 86.7 | 62.2 |
| prime adult | 21.1 | 12.6 | 37.8 |
| old adult | 0.0 | 0.7 | 0.0 |

TABLE 5

*U. spelaeus*, mortality data from the Bärenhöhle, Sibyllenhöhle, and Zoolithenhöhle for each of the three lower molars. The cohort juvenile includes Stiner's eruption/wear stages I-III, prime adults include stages IV-VII, and old adults stages VIII-IX.

### *The Sibyllenhöhle*

Atlas, scapula, astragalus, and metapodials were present in quantities which enabled the determination of sex ratios of adults ($n \geq 10$). While other elements such as humerus, radius, ulna, femur, and tibia are quite abundant (Table 7 in Appendix), most belonged to young animals.

In contrast to the Bärenhöhle, where males comprise about 70% of the adult death population, in the Sibyllenhöhle females outnumber males by as much as 4:1 ($\bar{x} = 77$; $\bar{x} = 80$; Figure 7 & Table 3).

At the Sibyllenhöhle the analysis of the age structure of the bear thanatocoenoses is made somewhat difficult by the small number of mandibles and teeth. The most common dental element, the $M_1$, is represented by only twenty specimens. It is clear, however, that late-juvenile bears (Stiner's stage III) are abundant (Figure 8 & Table 5). These are individuals which were probably just separated from their mother, and were just beginning to fend for themselves, and perhaps spending their first winter alone. This seems to be a critical transition period in modern brown bear populations which many individuals fail to survive (Bunnel & Tait, 1981). The absence of very young individuals (sta-

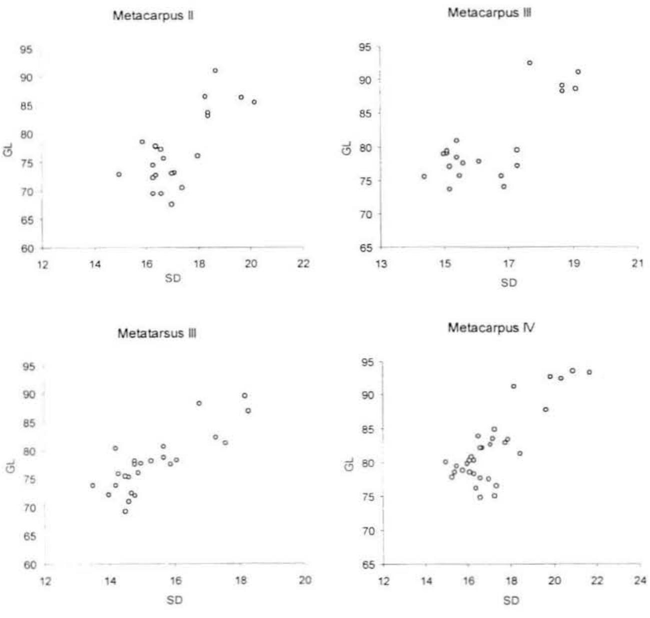

FIGURE 7

*U. spelaeus* from Sibyllenhöhle; bivariate plots of a number of skeletal elements. In all cases, females, represented by the group of smaller animals, are more abundant than males.

| element | E. Fraas, 1899 | SMNS collection, 2000 |
|---|---|---|
| complete skull | 7 | 3 |
| mandible | 86 | 29 |
| loose teeth | 652 | 136 |
| scapula | 23 | 18 |
| humerus | 25 | 18 |
| radius | 40 | 30 |
| ulna | 46 | 44 |
| femur | 21 | 12 |
| tibia | 29 | 24 |
| fibula | 19 | 14 |
| carpals | 45 | 32 |
| tarsals | 78 | 56 |
| metacarpal | 213 | 155 |
| metatarsal | 200 | 139 |
| phalanges | 118 | 75 |
| atlas | 26 | 16 |
| axis | 14 | 8 |
| ribs + vertebrae | 249 | 85 |

TABLE 7

*U. spelaeus*, number of specimens from the Sibyllenhöhle recovered and kept by Fraas, 1899 and those present today in the collection of the SMNS.

ges I and II) is conspicuous, but it may be due more to taphonomic than to demographic causes. This is strongly suggested by the analysis of the postcranial skeleton, which includes a relative high number of radii and humeri with early fusing epiphyses still open (Weinstock, unpublished data). The assemblage is also characterized by a scarcity of very old individuals (stages VIII-IX) and a relatively large proportion of prime adults (stages IV-VII). The mortality profile of the $M_1$ is reminiscent of a "living structure" (LS) pattern, which is not to be expected for denning bears (Kurtén, 1976; Stiner, 1994, 1998). A LS pattern is usually assumed to be produced by a catastrophic mortality or by the sum of discrete hunting events by ambush predators (Stiner, 1994). This would be the expected pattern if, for example, other predators attacked and killed the hibernating bears (Stiner, 1998).

Although about 80 bones (MNI= 4) of the lion *Panthera leo* were found at the site (Fraas, 1899), an unusually large number for a southern German

| skeletal element | n ♀ | n ♂ | % ♀ |
|---|---|---|---|
| atlas | 11 | 2 | 84.6 |
| scapula | 7 | 3 | 70.0 |
| mc II | 15 | 6 | 71.4 |
| mc III | 15 | 5 | 75.0 |
| mc IV | 26 | 6 | 81.2 |
| mc V | 16 | 8 | 66.6 |
| astragalus | 16 | 4 | 80.0 |
| mt III | 20 | 5 | 80.0 |
| mt IV | 22 | 5 | 81.5 |

TABLE 3

*U. spelaeus*, number of specimens of male and females and relative abundance of females in the Sibyllenhöhle.

cave site, it is uncertain whether the accumulation of the bear remains can be ascribed to this predator. It is conceivable that lions attacked hibernating/denning bears, as tigers in the Far East occasionally do (Heptner *et al.*, 1974). However, lions are not usually regarded as denning animals, and it is unclear how their own remains got to be part of the faunal assemblage. Bone remains from the denning hyaena *Crocuta crocuta* were also found in the Sibyllenhöhle, although in smaller numbers (n= 32, MNI= 2; Fraas, 1899).

In short, it is unclear whether the bear assemblage from the Sibyllenhöhle represents mostly individuals which died during hibernation or, rather, primarily from random predation *in situ*. In both cases, however, the sex ratio would be determined by the proportions of males and females which enter the cave before hibernation. The alternatives, that non-hibernating bears were killed by other carnivores and brought into the cave, or that the bear bones in Sibyl's Cave represent scavenged remains of individuals which died somewhere else, are supported neither by the relative common presence of prime adults, certainly not an easy prey for lions, hyenas or wolves, nor by the skeletal representation (Table 7 and Appendix).

### *The Zoolithenhöhle*

Not all of the *Ursus* skeletal elements from this site have been investigated yet, but preliminary results show already a very clear trend concerning sex-ratios. Canines, metapodials, humeri, and radii all indicate that adult and subadult males were very rare at the site (Figure 9 & Table 4). The percentage of females fluctuates, according to skeletal element, between 81% and 96% (x̄ = 90; x̄ = 87).

It must be stressed that, in contrast to the case of the Bärenhöhle and the Sibyllenhöhle, no part of the material retrieved in the 1971 excavations at the Zoolithenhöhle has been subsequently lost. This is important, since it demonstrates that a very biased sex-ratio must not be due to post-excavational taphonomic factors.

| element | ♀ | ♂ | %♀ |
|---|---|---|---|
| upper canine | 39 | 5 | 86.6 |
| lower canine | 27 | 6 | 81.8 |
| humerus | 39 | 2 | 95.0 |
| radius | 43 | 3 | 93.5 |
| intermedio- radiale | 45 | 10 | 81.8 |
| astragalus | 54 | 8 | 87.0 |
| mc II | 51 | 2 | 96.2 |
| mc III | 62 | 8 | 87.5 |
| mc IV | 42 | 6 | 87.5 |
| mc V | 55 | 3 | 94.8 |
| mt II | 47 | 6 | 88.6 |
| mt III | 46 | 4 | 92.0 |
| mt IV | 55 | 2 | 96.5 |

TABLE 4

*U. spelaeus*, number of specimens of male and females and relative abundance of females in the Zoolithenhöhle.

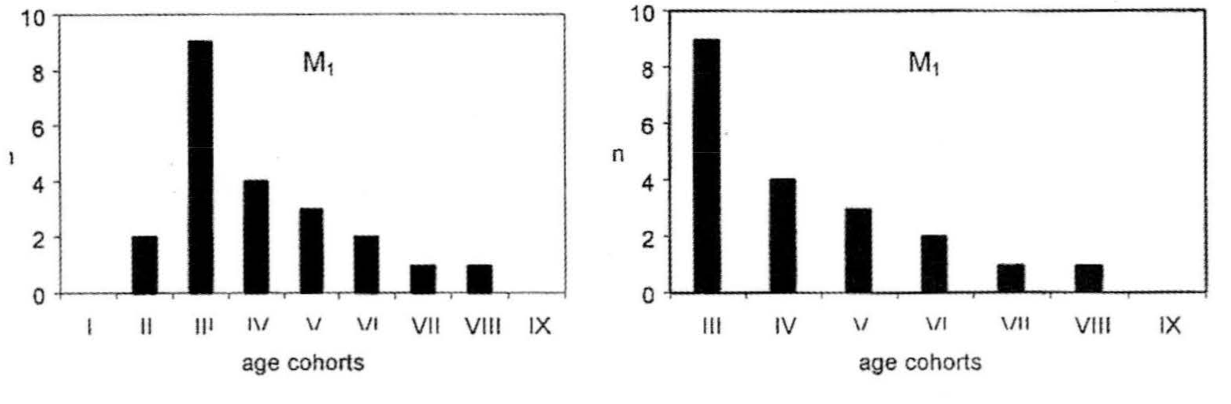

FIGURE 8

Age structure histogram for the Sibyllenhöhle bear population based on the eruption and occlusal wear of $M_1$ (due to the small number of M2 and M3 available, these were not included in the investigation). The graph at the right exclude cohorts I and II, the relative abundance of which could be influenced by taphonomic factors. Most individuals at this site are "young" (stage III). Prime adults (stages IV-VII) are nevertheless well represented, while "old adults" (stages VIII-IX) are relatively scarce.

The vast amounts of mandibles and dental material present at the Zoolithenhöhle allow for a reliable analysis of the age structure of the bears (Figure 10 & Table 5). Figure 10 shows the relative frequencies of nine age cohorts (Stiner, 1994, 1998) of the three mandibular molars. In these graphs, loose teeth are disregarded; their inclusion, however, leads to identical results. A number of facts are apparent. The distribution is, in contrast to the case of the Bärenhöhle, clearly unimodal peaking at cohort III. As mentioned above, these are probably older juveniles which had just become independent from their mother. Somewhat older individuals (stage IV) are also well represented. Prime adults other than those in stage IV (V-VII) are, on the other hand, very rare. New-born and very young animals (stages I-II) are relatively scarce. Since the fragile mandibles and bones of individuals in these age categories, especially in stage I, are more prone to mechanical destruction than those of older animals, this could have taphonomic rather than behavioural/demographic causes. All in all, juveniles (stages I-III) comprise 62%-87% of the assemblage, depending on which tooth is being analysed. However, the most striking characteristic of the age structure of the cave bears from the Zoolithenhöhle is the almost complete absence of very old individuals (stages VIII-IX). These age classes are usually well represented in other sites regarded as hibernation dens, such as the Bärenhöhle-Hohlenstein (see above) and Yarimburgaz (Stiner, 1998). Rather, the mortality profile from the Zoolithenhöhle resembles more the one from the Sibyllenhöhle (see above), although with a smaller proportion of prime-age adults.

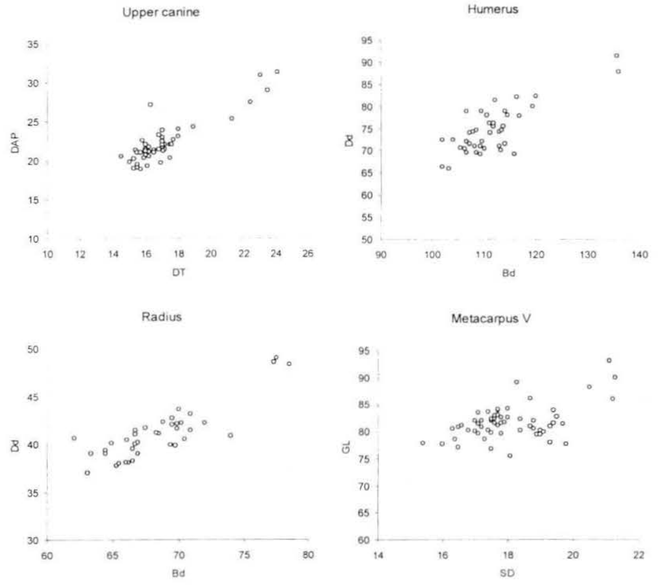

FIGURE 9

*U. spelaeus* from the Zoolithenhöhle; bivariate plots of a number of skeletal elements. All plots indicate an overwhelming overrepresentation of females.

The interpretation of the sex ratio and age structure of the cave bear assemblage from the Zoolithenhöhle in palaeobiological terms is not straightforward. On the basis of their location beneath a steep ledge, finds from the first (Esper's) excavations at the site were regarded as being remains from individuals which, while roaming around the cave, accidentally tumbled down and either died from the fall or were unable to climb out (Zapfe, 1954; Kurtén, 1976). The more recent excavations show, however, that the taphonomic history of many of the finds is probably more complicated. The large accumulations of bear bones in some parts of the cave are regarded as being caused by water transport (Groiss, 1972). The sources of these accumulations, however, are skeletons of bears which died elsewhere inside the cave (Groiss, 1972). Did most of these bears perish during hibernation? The relatively common presence of mandibles with erupting permanent canines would seem to point in this direction. In *Ursus arctos* the eruption of this tooth takes place between 12-14 months of age (Dittrich, 1960). Since brown bears are born in winter (November to February), these mandibles represent individuals who died during their second winter. Likewise, mandibles with still unerupted $M_1$ (i.e. younger than 5 months) also suggest winter mortality.

Ideally, if mortality did occur during hibernation, the age-at-death profile should be U-shaped, corresponding to an attritional mortality (Stiner, 1994, 1998). However, as Figure 10 shows, this is not the case. Nevertheless, there seems to be a lack of better alternatives to death during hibernation. While it is conceivable that some bears were attacked by other predators during hibernation, the mortality profile in the Zoolithenhöhle does not take the "living structure" pattern which would be expected in that case.

## DISCUSSION

Summing up from the preceding section: the sex ratio at Bärenhöhle is dominated by males; at Sibyllenhöhle females are in the majority; and at Zoolithenhöhle females comprise approx. 90% of the adult thanatocoenose. Furthermore, the cave bears from these sites differ not only in their sex ratios but in their age structure as well.

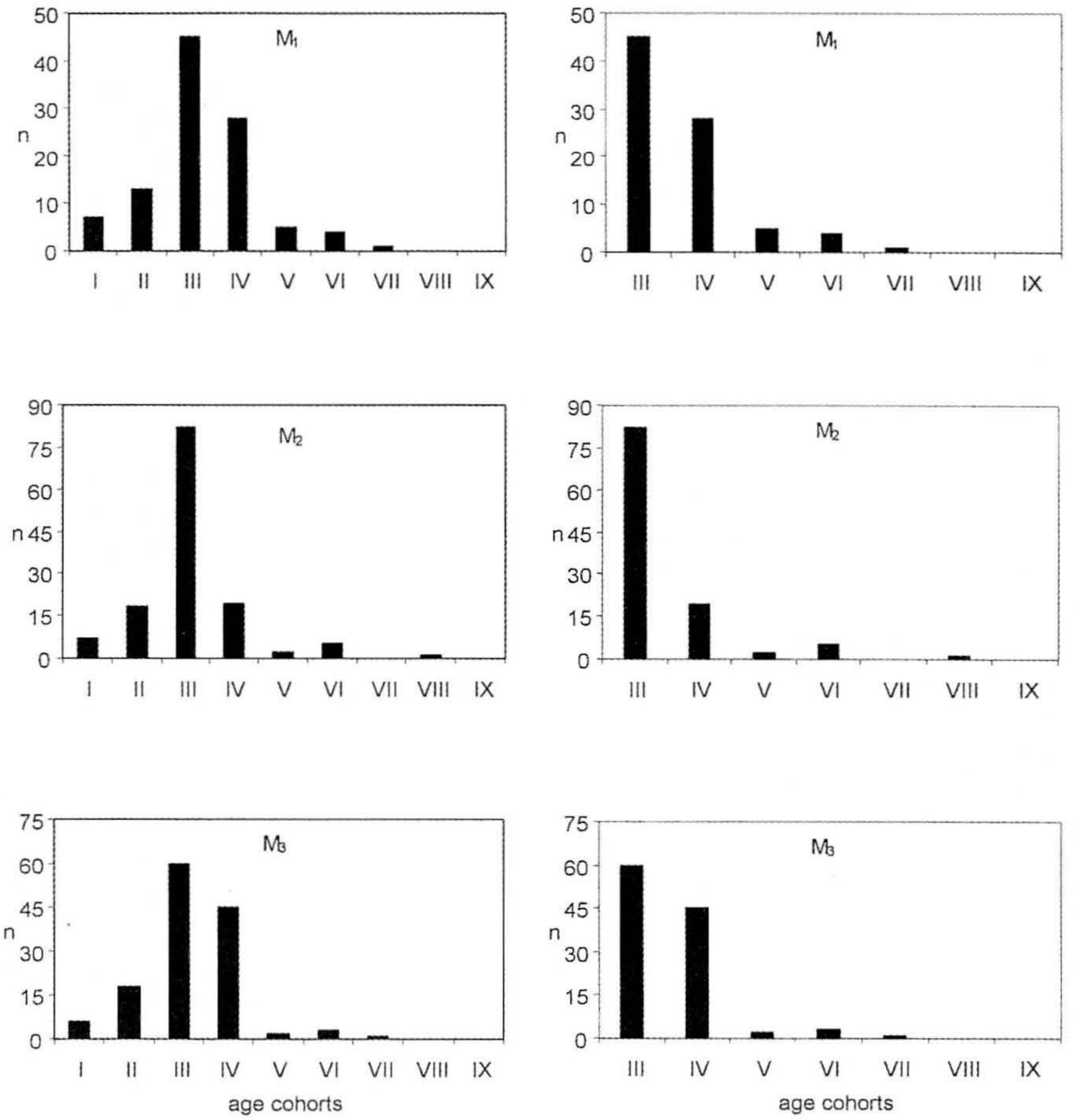

FIGURE 10

Age structure histogram for the Zoolithenhöhle bear population based on eruption and occlusal wear of mandibular molars. The graphs at the right exclude cohorts I and II, the relative abundance of which could be influenced by taphonomic factors. "Young" (stage III) and animals slightly older (Stage IV) comprise most of the population. Neonates (stages I-II) and "prime adults" (stages IV-VII) are very rare, while "old adults" (stages (VIII-IX) are virtually absent.

An interpretation of these differences in palaeobiological terms is not straightforward. Two caves located ca. 60 km apart, the Bärenhöhle and the Sibyllenhöhle, show very different demographic structures. If the model of Stiner *et al.* (1998) of sex ratios as indirect indicators of food seasonality is applied, we would have to conclude that environmental conditions around these two caves differed considerably. Furthermore, the overwhelming representation of females in the Zoolithenhöhle would imply that almost no males were hibernating in the Frankonian Alb. In our opinion, such conclusions are not very plausible. More important is the fact that whereas the paleodiet-model could account for female-biased or even sex ratios, it cannot explain male-dominated bear assemblages such as those from the Bärenhöhle, the upper levels of Mixnitz, or Arrikrutz, since this would imply that males were hibernating in higher numbers than pregnant females! (that the bear assemblage at Bärenhöhle represents indeed deaths which occurred during hibernation is strongly supported by its age structure; see above).

Therefore it can be concluded that, while the proportion of hibernating males and barren females *within a population* may have been affected to some extent by the seasonality of food resources, the sex ratios *within a cave* were determined by other factors.

Moreover, how seasonal the food resources of the cave bear were, is a matter of discussion. Stiner *et al.* (1998) argue that this species depended almost exclusively upon highly seasonal vegetal resources and invertebrates. However, according to recent isotopic investigations, meat contributed as much as 41%-78% of the metabolized carbon and nitrogen in *U. spelaeus* (Hildebrand *et al.* 1996; but see Bocherens *et al.* 1994).

As discussed above, Kurtén (1976) suggested that the variation in the intersite sex ratios could be explained by the size of the caves. Can the differences in the sex ratios between the Bärenhöhle Hohlenstein, Sibyllenhöhle, and the Zoolithenhöhle be thus explained?

In trying to answer this question there are obvious problems. Kurtén (1976) did not specify how cave size is to be measured. Is the area or the length of the cave important, or rather the size of its entrance? If defensibility was the criterion of choice, the existence of a narrow passage and/or small, almost inaccessible, recesses were probably more important than sheer size. The size and spaciousness of the Bärenhöhle and the Sibyllenhöhle is comparable but, as explained above, the sex ratios in these two caves differ markedly. Another cave in the Swabian Alb in southern Germany, the Große Grotte, is basically a spacious chamber, with an entrance 25 m broad. Nevertheless, and contrary to what according to Kurtén's hypothesis could be expected, the high percentage of bones of bear neonates in the assemblage suggests that it may have been mainly females which made use of the cave (Weinstock, 1999).

In any case, even if a relationship between sex ratios and cave properties does not seem to exist, a thorough investigation of this issue would necessarily involve taking into account the changes in topography and sediment deposition which have ocurred at each site since, and also during, the Pleistocene. Such an enterprise is beyond the scope of this paper.

Do the results presented here lend support to the hypothesis of Reisinger & Hohenegger (1998) about females looking for caves at higher elevations? It is obvious that the difference in altitude between the German sites, a couple of hundred meters, is nothing comparable to that recorded in the eastern Alps (see above), and variation in sex ratios caused by this factor is not likely to be observed here. Still, as shown above, sex ratios do vary, and they do it in a way unrelated to altitude: males do dominate the Bärenhöhle (467 m a.s.l.), and females are more common in the higher Sibyllenhöhle (763 m a.s.l.); however, the sex-ratio in the Zoolithenhöhle, which is located at a similar altitude as the Bärenhöhle (470 m a.s.l.), is, as mentioned above, strongly biased towards females. In other words, while it is possible that in the eastern Alps altitude does play a role in the variability of sex ratios, this is clearly not the case for the southern German sites; other factor(s) must be involved.

Are sex ratios perhaps related to differing mortality patterns? The details of the age distributions may differ (compare Figures 6, 8 & 10), but, when plotted on a tripolar diagram of the type proposed by Stiner, the assemblages of both the Bärenhöhle and the Zoolithenhöhle are juvenile-dominated (Figure 11 & Table 5), although their sex ratios are clearly biased towards males and females respectively. The Sibyllenhöhle, another female dominated assemblage, appears to belong to a different family pattern, namely that of a "living structure". Thus, in this broad sense, sex ratios and age structure do not seem to be correlated. However, even if mortality patterns at both Zoolithenhöhle and

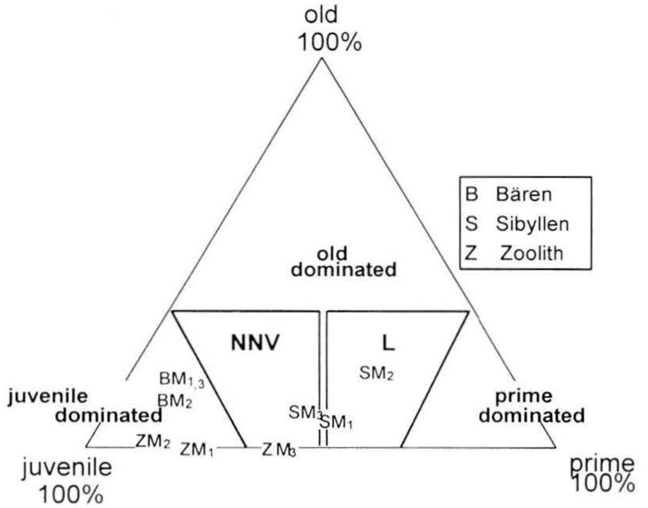

FIGURE 11

Tripolar age graph for the Bärenhöhle, Sibyllenhöhle, and Zoolithenhöhle. The first two sites show a juvenile-dominated mortality pattern, although their sex ratios are very different (male- and female-dominated respectively). The mortality pattern in Sibyllenhöhle falls within the "living structure" (LS) area of the triangle, which according to Stiner (1998) suggests that the assemblage was accumulated by predators such as *Panthera* or *Crocuta*. If ideed the bears at the Sibyllenhöhle were killed by predators, this must have occurred within the cave during hibernation, since the skeletal representation of *Ursus* argues against a transport of dead individuals into the site. Thus, in any case, the sex ratio should reflect the preferences of the bears themselves.

Bärenhöhle are assigned to the juvenile-dominated type, the clear difference in the relative abundance of very old animals between both sites is still in need of an explanation.

In Figure 12, the relative abundance of very old cave bears (stages VIII+IX) from the three sites presented in this study, plus the Brillenhöhle (south-western Germany), and Yarimburgaz (Turkey) is plotted against their respective mean sex ratio. There is a strong inverse correlation between these two variables: as the relative abundance of females in the assemblage increases, the proportional representation of old adults decreases. The interpretation of this pattern in palaeobiological terms is difficult. It seems to indicate that females failed to achieve a very old age as often as males (assuming that very old females had not the "habit" of dying in the open rather than within caves). If this was indeed the case, this would be an unusual demographical phenomenon among Ursids. Apparently, no such phenomenon has been recorded for either brown or black bears (in fact, as mentioned above, the mortality of male *U. arctos* increases relative to that of females from the sub-adult stage onwards; McNamee, 1997). In order to confirm this correlation, the demographic analysis of additional sites is needed. While data on tooth eruption and wear is available from a number of sites (e.g. Musil, 1965; Torres Pérez-Hidalgo, 1984; Andrews & Turner, 1992), the broad, more inclusive age categories incorporated in these cases are not comparable to those of Stiner (1994, 1998), especially for the older individuals.

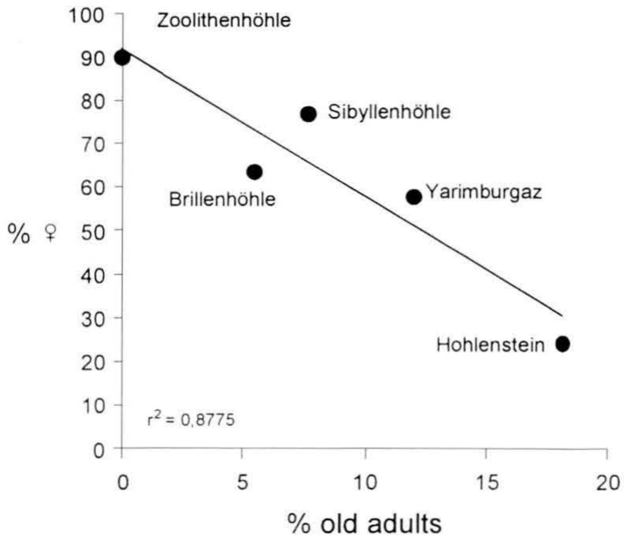

FIGURE 12

Relative abundance of old adult versus abundance of females based on the $M_1$ (Data for Brillenhöle after Boessneck & von den Driesch, 1973; for Yarimburgaz after Stiner, 1998 and Stiner *et al.*, 1998). A strong inverse correlation is apparent which, if the trend is supported by additional finds in the future, may indicate that males reached an old age more often than females.

The use of tripolar diagrams is certainly useful for the interpretation of mortality patterns of different species (see Stiner, 1990, 1994), but assemblages belonging to the same mortality pattern family (e.g. juvenile-dominated) may still exhibit differences which are a potentially useful source of palaeobiological information.

Summing up, the sex ratios of cave bears in Eurasian sites are highly variable. While the seasonality of the food supplies may have been responsible for the relative frequency of hibernating males within a population, it cannot explain the sex ratios within a cave. In our opinion, Kurtén (1976) was right on varying sex ratios between caves being a product of the choice by the bears themselves. However, it is not apparent that the size of the cave was the criterion according to which the bears choose their hibernation site.

What was the criterion then? We still do not know. Potentially relevant information for recent bear populations is seemenly not available. For European brown bears, caves are not the first choice as denning/hibernation places: only a small minority (ca. 12.7%) uses them for such purpose (Jakubiec, 1993). Whether among these relatively few individuals males and females select different kind of caves remains unknown.

## ACKNOWLEDGEMENTS

I would like to thank Th. Rathgeber (Natural History Museum, Stuttgart) for important information about the history of the collections from the Bärenhöhle and the Sibyllenhöhle. I am also grateful to Prof. Th. Groiss (Erlangen) for allowing me to examine the material from the Zoolithenhöhle. Thanks are due to B. Dechert, C. Pasda, K. Pasda, H.-P. Uerpmann, and R. Ziegler who read and commented on earlier versions of the paper.

## APPENDIX

The purpose of this appendix is to show that, contrary to the opinion of Adam (quoted in Kurtén, 1964, 1976), sex ratios at Bärenhöhle and Sibyllenhöhle are not a product of their post-excavation history.

| element* | O. Fraas, 1862 | SMNS collection, 2000 |
|---|---|---|
| skulls | 40 | 7 |
| mandible | 375 | 152 |
| scapula | 100 | 9 |
| humerus | 150 | 25 |
| radius | 130 | 45 |
| ulna | 130 | 33 |
| femur | 200 | 30 |
| tibia | 150 | 51 |
| fibula | 80 | 24 |
| atlas | 90 | 36 |
| axis | 80 | 25 |
| cervical vertebra | 200 | 120 |
| total | 3587 | 2556 |

* Fraas (1862) does not present data for elements such as astragalus, calcaneus, carpals, tarsals, phalanges, and vertebrae other than cervical; nevertheless, these elements are present in the SMNS collection.

TABLE 6

*U. spelaeus*, number of specimens from the Bärenhöhle recovered and kept by Fraas, 1862 and those present today in the collection of the SMNS.

Concerning the Bärenhöhle: the statement that O. Fraas excavated the site together with the Swabian Cave Society in 1861 is simply not true, since this Society was only established in 1889 (T. Rathgeber personal communication). It is true, however, that nowadays a considerable proportion of the original material is missing from the collection (Table 6). This is a result of material having been given away to museums, collectors, and researchers in Germany and abroad. An exact record of the material thus lost for the SMNS does not exist, and the selection criteria employed to choose the material being given away are unknown. Nevertheless, it is improbable that those selection criteria, if there were any, were applied so consistently so as to produce an artificial, similar sex ratio in most skeletal elements (Table 2). It seems more probable that the selection had more to do with the state of preservation of the remains, i.e. those specimens being somewhat more damaged were preferentially given away. Fraas (1862) was aware of the clear variation in the size of cave bears from Bärenhöhle; some bones, usually complete humerus, radius, ulna, and femur, were even labelled as belonging to either "Form A" (large) or "Form B" (small). Moreover, he recognized that this large size difference was caused by sexual dimorphism (Fraas, 1862).

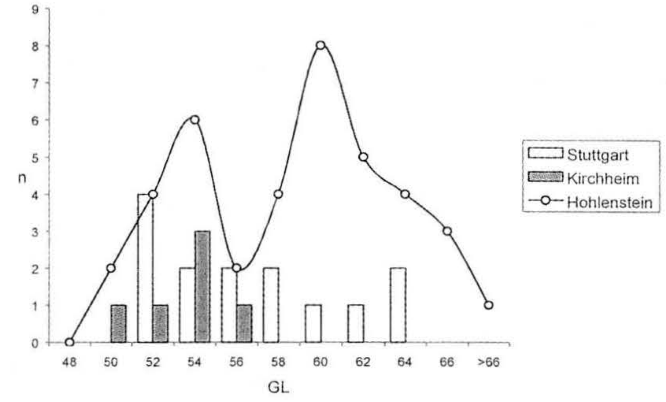

FIGURE 13

Relative frequencies of the greatest length of the astragalus in the material from the Sibyllenhöhle originally stored at the SMNS and in the material returned to Stuttgart from Kirchheim/Teck (see Text). Superimposed is the distribution of the astragali in the Bärenhöhle, which shows a bimodal distribution reflecting the presence of males and females.

In the case of Sibyllenhöhle, it can be clearly demonstrated that the sex ratios are not a result of the material having being divided between the Museum and the Swabian Cave Society, as Adam (quoted in Kurtén, 1976) asserted. After the dissolution of the Society in the first years of the twentieth century, most of its material from the Sibyllenhöhle was deposited at the local museum in Kirchheim/Teck. In the second half of the twentieth century most of these remains were transferred to the SMNS. To be sure, some part of the original material is still missing, mainly skulls, mandibles, teeth, and femora which are easily recognizable for the amateur and the layman and thus more attractive, and it is probable that they remained in the private collections of the Society's members (Table 7).

Since the material returned to the SMNS was kept separate from that originally stored there at the turn of the century, the hypothesis that the Swabian Cave Society got most of the male specimens can be easily tested. As Figure 13 shows, the astragali originally kept by the Society and subsequently returned to the SMNS are of small size. When compared to the distribution at Bärenhöhle, which is distinctly bimodal, it is clear that most if not all of the astragali from Kirchheim/Teck must come from females.

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