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Age structure and sex ratio of cave bears in the Zoolithenhöhle, southern Germany

Estructura de edades y proporción de sexos del Oso de las Cavernas de Zoolithenhöhle, Alemania

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ABSTRACT

This paper reports the results of the study of age and sexual composition of the cave bear (*Ursus spelaeus*) 'population' of the Zoolithenhöhle, a classic cave site in Bavaria, southern Germany. Radiocarbon dating indicates that the assemblage dates to c. 29-24 ka BP. The osteometrical analysis shows that the great majority (ca. 90%) of the bears denning in the site were females. The tooth eruption and wear reveal the presence of a large proportion of young and some mature animals but a marked paucity of very old adults. The reason(s) for this very skewed sex ratio and the almost total absence of senile individuals is unclear.

Key words: cave bears, demography, sexual dimorphism, ageing, Germany

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INTRODUCTION

In the last 20 years there has been an interesting shift in cave bear research (both *Ursus spelaeus* and *U. deningeri*) from almost purely anatomical and palaeopathological questions to more palaeobiologically oriented studies such as those focusing on demography, diet, or evolution. Witness to this shift are the numerous publications based on Austrian, British, Spanish, and Turkish collections (e.g. ANDREWS & TURNER, 1992; FERNÁNDEZ MOSQUERA, 1998; GRANDAL-d'ANGLADE, 1993; GRANDAL-d'ANGLADE & VIDAL ROMANÍ, 1997; GROISS, 1994; RABEDER, 1983, 1991; REISINGER & HOHENEGGER, 1998; STINER, 1998; STINER *et al.*, 1998; TORRES PÉREZ-HIDALGO, 1984; TORRES PÉREZ-HIDALGO *et al.*, 1991). It is only through understanding of the palaeobiology of this taxon that we will be able, eventually, to explore some of the many questions that remain to be answered, such as the reasons for its relatively restricted (basically European) geographical range, or the cause(s) for its extinction.

Interestingly, southern Germany, while being one of the 'classic' cave bear areas, has not contributed much to this new research. It was, in fact, in southern Germany that the earliest discoveries of cave bear bones were made by J. Esper in 1774, and the holotype specimen of *Ursus spelaeus* comes from the Zoolithenhöhle (also known as the Gaillenreuth cave), a site in the Franconian Jura in south-eastern Germany (ROSENMÜLLER & HEINROTH, 1794). Some sites in the

Swabian Alb (Baden-Württemberg, south-western Germany), notably the Bärenhöhle-Hohlenstein in the Lone Valley and the Sibyllenhöhle near the town of Kirchheim/Teck (figure 1), have been famous for their vast amount of cave bear remains since the second half of the 19th century, when they were presented in publications by O. FRAAS (1862) and E. FRAAS (1899) respectively. In spite of this long history, very few investigations on cave bears (either *Ursus spelaeus* or *U. deningeri*) from southern Germany have been carried out – or published – in the last few decades (see BOESSNECK & von den DRIESCH, 1973; WEINSTOCK, 2000a).

One of the reasons for the paucity of studies on cave bears from southern Germany is probably the destruction or dispersal of some of the most important collections, such as that of the old excavations at the Zoolithenhöhle, the Bärenhöhle and the Sibyllenhöhle. According to K.-D. Adam, former curator of Quaternary Mammals in the State Museum for Natural History in Stuttgart, Germany, large parts of the collections from the last two of these sites were lost, or selectively removed, so rendering any study at the population level useless (KURTÉN, 1976). Nonetheless, these collections remain of value (WEINSTOCK, 2000a). In this contribution, however, I concentrate on the material from the Zoolithenhöhle that was recovered from more recent excavations by Heller and Groiss in 1971 (HELLER, 1972; GROISS, 1979). While the investigation of this material has not yet been completed, enough preliminary informa-



Figure 1. Map of Germany showing the locations of the Zoolithenhöhle, Bärenhöhle and Sibyllenhöhle.

tion is available to suggest some very interesting patterns in the sex ratio and age structure of this population.

THE ZOOLITHENHÖHLE

The Zoolithenhöhle is located near Burggailenreuth (470m above sea level) in the Franconian Alb, Bavaria. The structure of the Zoolithenhöhle is complicated (figure 2). The entrance is located in the North and from here a large chamber extends south for about 40m. Beyond runs a maze of irregular chambers, which are often interconnected through narrow, sometimes vertical passages. The cave owes its name to the word 'zooliths' that 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. From the very abundant faunal material from the early investigations, the whereabouts of only a small fraction is known (HELLER, 1972; Groiss, personal communication). In 1971, new excavations were carried out in a number of different areas which had not been dug or disturbed previously (GROISS, 1972). Again, considerable quantities of faunal material dating to the last glacial were recovered, consisting mostly of *Ursus spelaeus*, but also including other taxa, notably *Gulo gulo*, *Canis lupus*,

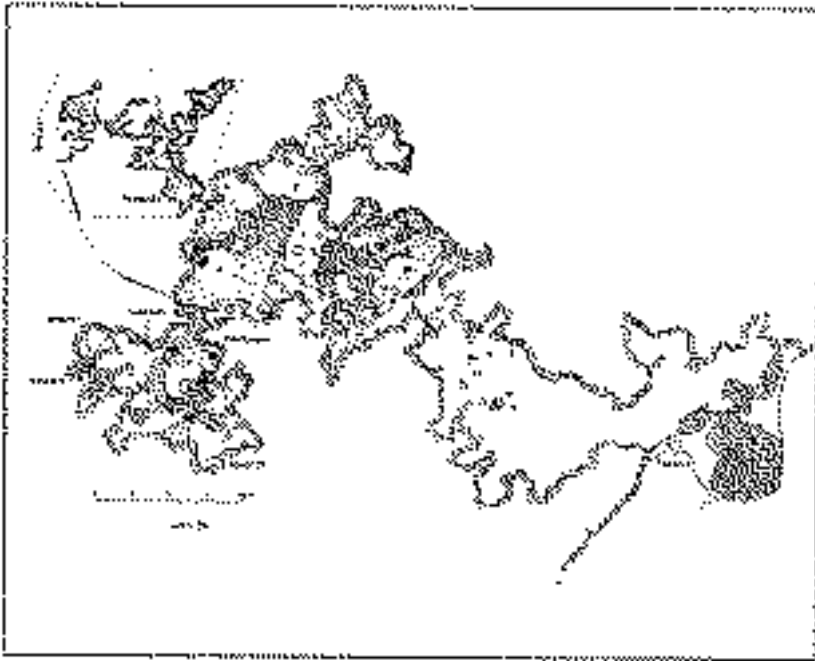


Figure 2. The Zoolithenhöhle (after NIGGEMEYER & SCHUBERT, 1972).

Crocuta crocuta, and *Panthera leo* (HELLER, 1972; GROISS, 1979). Absolute radiocarbon 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. This size difference is apparent in the width and depth of the long bones. However, the degree of sexual dimorphism varies, according to species, between 10-20% to 50% (STIRLING, 1993). A clear sexual dimorphism exists also in the canines (KOBAYASHI, 1949). Thus osteometrical data can be used to establish the relative proportions of both sexes in an

assemblage. In this investigation, measurements were taken on a number of postcranial limb elements showing fused epiphyses (humerus, radius, intermedio-radiale, astragalus, metacarpus II-V, and metatarsus II-IV), as well as on the lower and upper canines. Measurements were taken with a pair of digital callipers to the nearest 0.1mm following the definitions of GRANDAL-d'ANGLADE (1993) and von den DRIESCH (1976).

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 be used to calculate sex ratios. Sex ratios were cal-

culated for each of the postcranial elements and the canines. 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 (c.f. GRANDAL-d'ANGLADE & VIDAL ROMANÍ, 1997; WEINSTOCK, 2000a, 2000b; see below). These variations may sometimes be related to sample size but they are also a result of the fact that different skeletal elements represent somewhat different age classes (WEINSTOCK, 2000b).

The age structure was analysed using the method developed by STINER (1994, 1998). In this method, each tooth is assigned to one of nine different categories or cohorts (I-IX, from young to old) according to its stage of eruption and/or its occlusal wear (figure 3). Stage I, for example, includes all permanent teeth from the germ stage to those with root formation up to 50% complete. Stage II comprises

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 dentin is exposed. At the other extreme, stages VIII and IX include teeth which are very heavily worn, with little or no enamel remaining on its occlusal surface, and where the pulp cavities are frequently exposed (STINER, 1998). These nine cohorts can be collapsed into three age stages: juvenile (I-III), prime adult (IV-VII), and old adult (VIII-IX) (STINER, 1998).

In the Zoolithenhöhle mandibles and loose mandibular teeth are much more abundant than maxillaries and maxillary teeth, and therefore the age structure analysis was based only on the former. It must be stressed that mandibles and loose teeth from individuals in cohorts I and II (i.e. very young animals) are less resistant

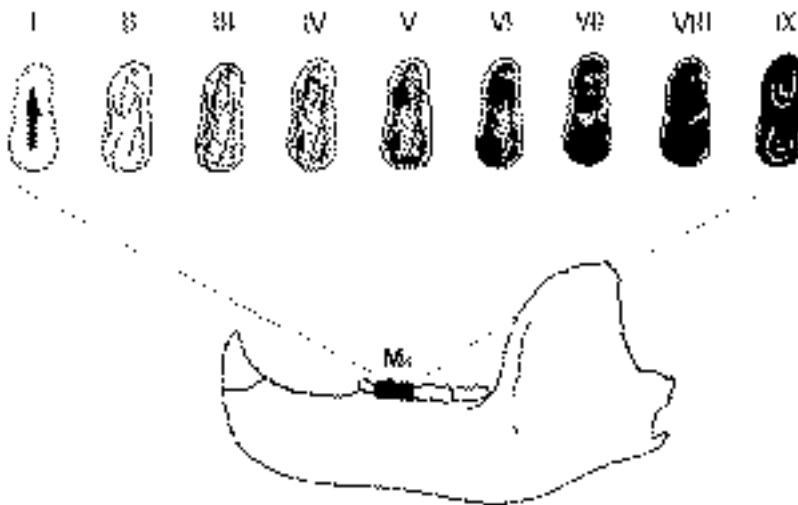


Figure 3. Wear stages (cohorts) of M1 (after STINER, 1998).

to mechanical damage than those in older cohorts and therefore this age group may be underrepresented due to post-depositional events.

RESULTS

Sex ratios

As mentioned above, not all of the *Ursus* skeletal elements from this site have been investigated yet. Nevertheless, preliminary results show 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 4 and table 1). The percentage of females fluctuates according to skeletal element varying between 81% and 96% (mean = 90%; median = 87%). It must be stressed that no part of the material retrieved in the 1971 excavations at the Zoolithenhöhle has been subsequently lost, in contrast to the other south

German sites. This is important as it demonstrates that a very biased sex ratio need not be attributed to post-excavational factors.

Age structure

The large numbers of mandibles and quantity of dental material present at the Zoolithenhöhle allow a reliable analysis of the age structure of the bears (figure 5). figure 5 shows the relative frequencies of nine age cohorts (STINER, 1994, 1998) based on 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 clearly unimodal with the peak at cohort III. 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, however, very rare. New-born and very young

Element	N female	N male	% females
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 1. Number of bones from male and female cave bears and relative abundance of females in the Zoolithenhöhle. Counts made from bivariate plots.

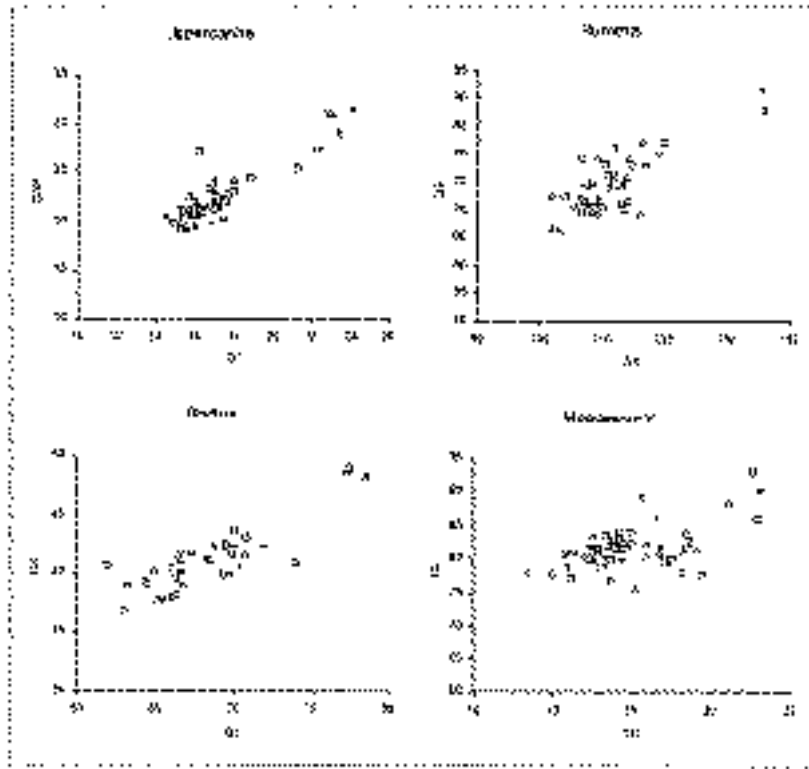


Figure 4. Examples of bivariate plots of different skeletal elements used to calculate sex ratios.

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 or 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 at other sites regarded as hibernation dens, such as the Bärenhöhle-Hohlenstein (WEINSTOCK, 2000a) and Yarimburgaz (STINER, 1998).

DISCUSSION

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 original excavations (ESPER, 1774) were regarded as being rests from individuals which, while roa-

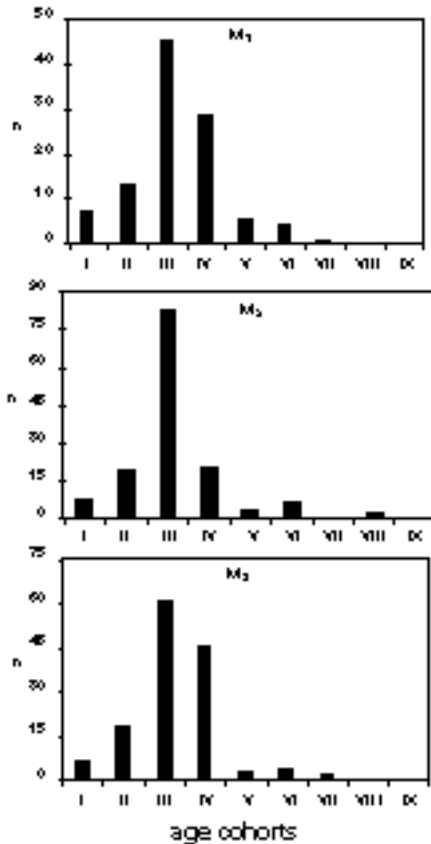


Figure 5: Age structure histogram for the Zoolithenhöhle bear population based on eruption and occlusal wear of mandibular molars. 'Young' (stage III) and animals slightly older (Stage IV) comprise most of the population. Neonates (stages I-II) and 'prime adults' (stages IV-VII) are very rare, while 'old adults' (stages VIII-IX) are virtually absent.

ming around the cave, accidentally tumbled down and either died from the fall or were unable to climb out (KURTÉN, 1976; ZAPFE, 1954). 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, nonetheless, are skeletons of bears that died elsewhere inside the cave (GROISS, 1972). Did most of these bears therefore 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 M1 (i.e. younger than 5 months) also suggest winter mortality.

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 5 shows, this is not the case. On the other hand, 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 (STINER, 1998).

Perhaps the most puzzling aspect of the assemblage is the very biased sex ratio in the cave, with females comprising between 82%-96%, depending on the skeletal element analyzed. Great variability in cave bear sex ratios has been observed between assemblages from different sites (e.g. KURTÉN, 1976; WEINSTOCK, 2000a) but has not yet been satisfactorily explained.

ned (WEINSTOCK, 2000a). The assemblage from the Zoolithenhöhle shows that this variability cannot be dismissed as a product of post-excavation factors; it must have some palaeobiological significance.

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