

FOSSIL POPULATION STRUCTURE AND MORTALITY OF THE CAVE BEAR FROM THE MOKRICA CAVE (NORTH SLOVENIA)

STRUKTURA FOSILNE POPULACIJE IN UMRLJIVOST JAMSKEGA MEDVEDA IZ MOKRIŠKE JAME (SEVERNA SLOVENIJA)

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Abstract

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Irena Debeljak: Fossil population structure and mortality of the cave bear from the Mokrica cave (North Slovenia)

The fossil population structure of the cave bear from the Mokrica cave was evaluated to provide new data concerning the behaviour and mortality of this extinct species. Age at death was estimated for 128 different individuals by analysing cementum increments, root formation and crown wear of left M_1 teeth. After the frequency distribution of specimens through one-year intervals, the mortality trends can be estimated for various lifetime periods, and interpreted in accordance with data for present-day bears. The original death assemblage was presumably juvenile-dominated. Extremely fragile molars of less than 6 month old cubs did not get preserved. Yearlings are the most numerous age class in the fossil population from the Mokrica cave. Mortality drastically dropped after cave bears survived their first hibernation in the second winter. The lowest mortality rate was observed in the 9-15 years age group, when cave bears would be expected to be in their prime. The oldest age recorded by cementum analysis is approximately 30 years, which indicates that the maximum life span was similar to present-day bears. Study of dental tissues shows that the mortality in the cave was seasonally restricted – the majority of deaths in the cave occurred during winter and in early spring. Sex structure of the fossil population has been studied on the sample of 750 canines. The significantly higher proportion of males in the group of older juveniles and subadults could be explained by the fact that the weaning period is more critical for males also in present-day bears. In young adults and prime adults the mortality was presumably higher in females. The sex structure of adult bears, especially in the sample of older individuals, indicates that the Mokrica cave was used as winter den mostly by solitary males.

Keywords: cave bear, mortality, age structure, sex structure, cementum.

Izvleček

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Irena Debeljak: Struktura fosilne populacije in umrljivost jamskega medveda iz Mokriške jame (severna Slovenija):

Struktura fosilne populacije jamskega medveda iz Mokriške jame je bila proučena z namenom, da bi dobili nove podatke o vedenju in umrljivosti te izumrle vrste. Starost ob smrti je bila ocenjena za 128 različnih osebkov, in sicer na podlagi analize cementnih prirastnic, formiranosti korenine in obrabe krone levih M_1 zob. Po frekvenčni distribuciji primerkov v enoletnih intervalih lahko ocenimo trend umrljivosti v različnih življenjskih obdobjih in jih interpretiramo glede na podatke o današnjih medvedih. V prvotni mrtvi združbi so po vsej verjetnosti prevladovali mladiči. Izjemno krhki molarji manj kot 6 mesecev starih živali se niso fosilno ohranili. Enoletniki so najbolj številčno zastopana starostna skupina v fosilni populaciji iz Mokriške jame. Umrljivost je drastično upadla, potem ko so jamski medvedi preživel svojo prvo hibernacijo v drugi zimi. Najnižja stopnja umrljivosti je bila ugotovljena za starostno obdobje 9-15 let, ko so bili jamski medvedi očitno na vrhuncu moči. Z analizo cementa ugotovljena najstarejša starost znaša okoli 30 let, kar kaže, da je bila najdaljša življenjska doba podobna kot pri današnjih medvedih. Analiza zobnih tkiv je pokazala, da je bila umrljivost v jami sezonsko omejena – večina živali je poginila pozimi in zgodaj spomladi. Spolna struktura je bila raziskana na vzorcu 750 podočnikov. Izrazito večji delež samcev v skupini starejših mladičev in napol odraslih živali bi lahko razložili z dejstvom, da je tudi pri današnjih medvedih obdobje osamosvajanja bolj kritično za samce. Pri mlajših odraslih in zrelih odraslih živalih je bila umrljivost verjetno večja pri samicah. Spolna struktura odraslih medvedov, še posebej starejših živali, kaže, da so Mokriško jamo kot zimski brolg večinoma zasedali samotarski samci.

Ključne besede: jamski medved, umrljivost, starostna struktura, spolna struktura, cement.

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INTRODUCTION

Age and sex structure of the fossil population of the cave bear (*Ursus spelaeus*) from the Mokrica cave (Mokriška jama) was studied to generate new data and insights concerning the behaviour and mortality of this extinct species.

Mokrica cave is located in the Kamnik-Savinja Alps (N Slovenia) between Mokrica and Košutna, at an altitude of 1500 metres, about 1000 metres above Kamniška Bistrica river valley. It is horizontal, about 45 metres long and 7 to 20 metres wide horizontal cave, formed in Triassic limestone. Its entrance faces in Northeast. Mokrica cave, also called 'Bear cave' (Medvedja jama), has been well known since the early 1800's for its rich accumulation of cave bear remains. Systematic excavations were carried out by Mitja Brodar during 1954-1956 and 1960 in the entrance part of the cave (Brodar, 1959). Ten strata (5-14) of Pleistocene sediments containing cave bear remains have been recognized there, approximately 6 me-

tres thick. The majority of cave bear remains (isolated teeth and fragmented bones) were recovered from strata 6 and 7. Systematic palaeontological analysis of the material was carried out by Rakovec (1967). Cave bear dominates the assemblage; fossil remains of other animals (wolf, cave lion and ibex) are scarce and have been found only in stratum 7 (Rakovec, 1967). Artefacts from strata 6 and 7 have been attributed to the Aurignacian cultural level (Brodar, 1959). Findings of M. Brodar suggest that cave bear remains mostly derive from the Middle Würmian period (OIS 3).

Data on the cave bear population structure from the Mokrica cave can be compared to data (Debeljak, 2004) obtained from a similar study of cave bear material from another well-known Aurignacian station and Middle Würmian high Alpine cave bear site Potočka zijalka, which is situated just 17 km away from the Mokrica cave.

MATERIAL AND METHODS

Fossil population structure of the cave bear from the Mokrica cave has been derived from teeth that were collected along with other fossil material during Brodar's excavations more than 50 years ago. The majority of the material is stored in the Natural History Museum in Ljubljana, but some specimens are kept in the palaeontological collection of the Department of Geology, University in Ljubljana. The sediment has not been water-sieved during the excavations in the Mokrica cave. For this reason, milk teeth were not recovered and it is therefore not possible to study the mortality of cubs younger than 6 months.

I analysed fossil population age structure using first lower permanent molars (M_1), both isolated and still attached in mandibles. Only left specimens were analysed to prevent the doubling of data for the same individuals. For 107 isolated M_1 specimens age at death was determined by the analysis of dental tissues (dentine and cementum) in cross sections through the root, about 7.5 mm below the crown. Thin sections and etched/coloured ground sections were prepared for all samples (for laboratory techniques see Debeljak, 1996; 2000). In juvenile specimens I measured the thickness of the root wall. The relative width of pulp canals and dentine increments can be used as criteria to assess individual age in juveniles and subadults (up to the 4th year). The individual age of all teeth belonging to animals older than 1 year was de-

termined by counting cementum increments. This is the most reliable and objective method for determining individual age of many mammals and has long been used routinely in present-day bears as well (see Debeljak, 2000 and references therein). Cementum is a bone-like tissue that is continuously deposited on the surface of tooth roots throughout life. Dental cementum is composed of so-called 'winter' and 'summer' layers, similar to growth rings in trees (Fig. 1). After the nature of the outermost cementum increment, it is sometimes possible to determine even the season of death. Dental tissues of 21 left M_1 teeth still attached in mandibles have not been microscopically examined, because it would be impossible to extract them without visible damage to the jawbone. For these specimens individual age was roughly estimated by comparing their crown wear patterns to the teeth of known individual age. Altogether, age at death has been estimated for 128 different individuals.

In bears, sex can be determined after dimensions of canines. Several studies indicate that there is no significant difference between measurements of lower and upper canines (Koby, 1949; Kurtén, 1955; Rabeder, 2001). Both upper and lower specimens were included in the analysed sample, because it is often impossible to distinguish between them when they are damaged or heavily worn, especially in the group of older individuals. Measurements of crown width of 377 undamaged specimens were

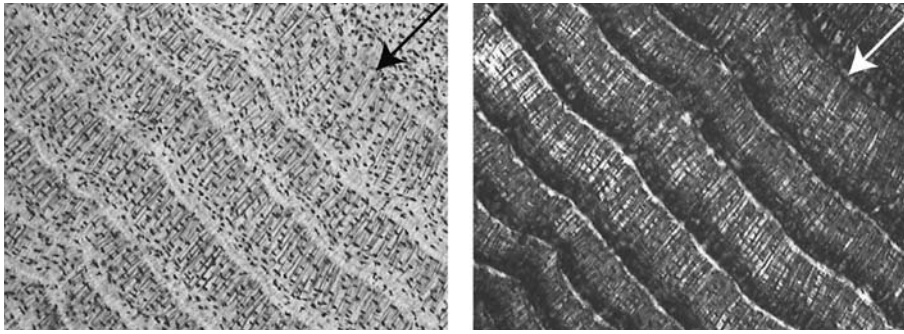


Fig. 1: Dental cementum in the cave bear M_1 (inv. number M. 4228) from the Mokrica cave. 'Summer' and 'winter' increments can be seen, divided by lines of arrested growth. Dark dots are cementocyte lacunae. An arrow indicates the direction of cementum deposition. Thin section; plane-polarized light (left image) and cross-polarized light (right image). The field is about 0.8 mm wide.

taken at the crown base. The histogram of crown width shows clear bimodal distribution (Fig. 2); specimens

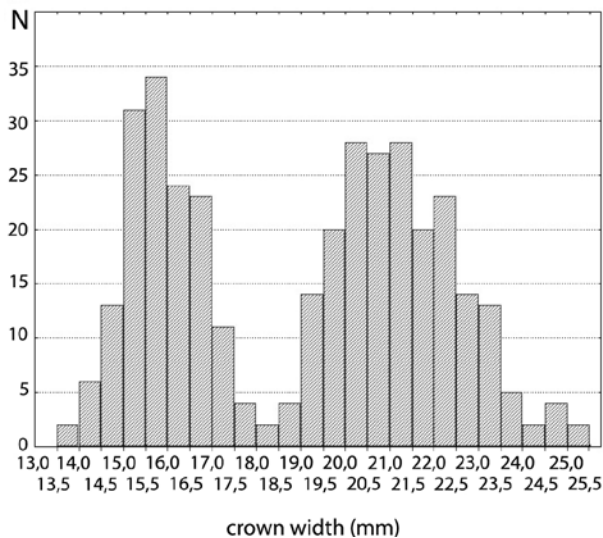


Fig. 2: Histogram for crown width (in mm) of upper and lower canines from the Mokrica cave. Bimodal distribution shows marked sexual dimorphism.

with crown width larger than 18.5 mm were attributed to males and specimens with crown width smaller than 18

mm as belonging to females. Mean value of crown width is 21.3 mm for males and 15.8 mm for females. Also Kurtén (1955) determined mean size difference of more than 5 mm and joint overlap of less than 1 per cent in the Mixnitz sample. Sexual dimorphism is so well pronounced in canines that usually even those specimens that are too damaged or worn to be measured accurately can be sexed based on their overall dimensions. Altogether, population sex structure (males to females

ratio) has been established on the sample of 750 canines (isolated and those still attached in jawbones) of individuals older than 18 months. Canines of yearlings were omitted from the study because they are composed only of a hollow crown cone which is usually damaged in the lowermost part and therefore difficult to measure.

All the canines had been previously separated into 3 different age classes. Canines with the root widely open at the apex are classified into the group of older juveniles and subadults. Our studies of canines, whose individual age has been determined by cementum analysis, show that their root closed at the age of 5-6 years. Canines with a closed root can be therefore all assigned adult status. Adult specimens were further divided into two groups: specimens with slightly to moderately worn crowns, and specimens with markedly to heavily worn crowns. There is no clear distinction between the two groups. In canines, crown wear was quite erratic and heavy wear does not necessarily indicate old age. Canines could have been broken and pathologically worn even by prime adults. However, preliminary study of dental cementum in canines from Divje babe cave indicates that the majority of specimens from the first group belonged to 5-15-year-old individuals (young- and prime adults) and specimens from the second group to 15-25-year-old individuals (older adults).

RESULTS AND DISCUSSION

AGE STRUCTURE:

The results of the individual age analysis of 107 isolated left M_1 teeth are shown in the frequency histogram of individuals in one-year age classes (Fig. 3). Frequencies

in some of them are not integers because, for example, in the case of a specimen with age estimation of 14-15 years, one half was attributed to the class of 14-year-olds and one half to 15-year-olds. From this profile, the course

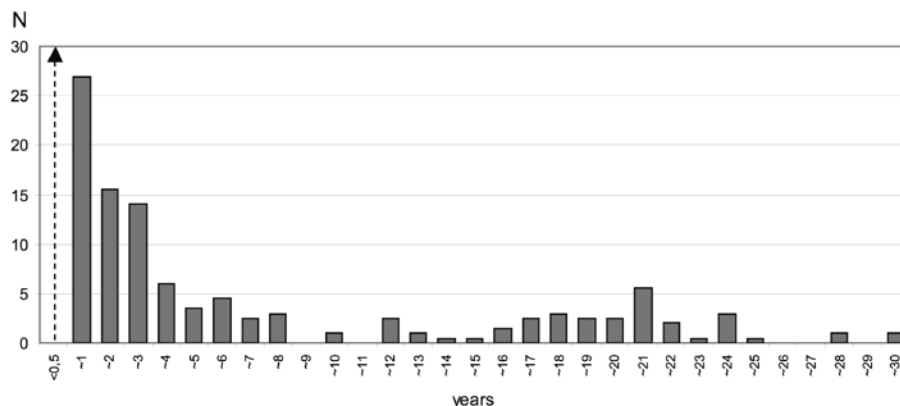


Fig. 3: 'Mortality profile' – frequency distribution of isolated left lower M_1 teeth through one-year intervals ($N=107$). Extremely fragile molars of less than 6 month old cubs were not preserved. The supposed highest mortality in this age group is indicated by an arrow.

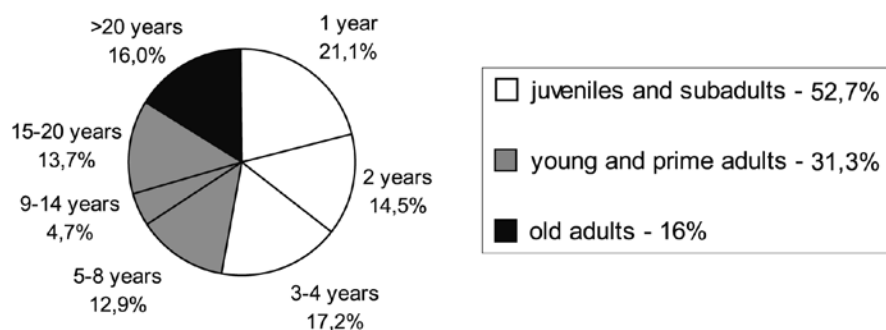


Fig. 4: Pie chart with proportions of left M_1 teeth; isolated and still attached in mandibles ($N=128$) from different age groups.

of mortality in the cave can be estimated for various life periods or age groups. Fig. 4 shows the proportions of different age classes in the sample of 128 left M_1 specimens, including both isolated and those still attached in the jawbones. Yearlings and 2-year-olds are considered to be juveniles, 3-4-year-olds are subadults, 5-8-year-old individuals young adults, 9-20-year-olds prime adults and those older than 20 years old adults (Craighead *et al.*, 1995). The mortality in the main age groups will be discussed briefly:

Like in present-day bears, cave bear cubs were born in a winter den, most probably in December or January. Still unerupted M_1 crowns of 2-4-month-old cubs that died in the first winter, before the onset of spring, were hollow and fragile as an egg shell. They were completely destroyed *post mortem* and are therefore not represented in the analysed sample (Fig. 3). In Divje babe cave, where all the sediment has been water-sieved during the excavations, a very large number of milk teeth have been recovered. The analysis of fossil population structure from Divje babe I site (Debeljak, 2002) indicated that the mortality

was highest for this youngest age group. Most likely, this was the case in the Mokrica cave as well, which is indicated by an arrow in Fig. 3.

Yearlings (9-15-month-old individuals) are the most numerous age group in the fossil population with a 21.1% share (Figs. 3, 4), suggesting that the mortality in the second winter was very high, although presumably lower than the mortality in the first winter, as explained above. Very high mortality in yearlings may be at least partly attributable to different predators, such as wolves and male bears. Cannibalistic behaviour of adult males and their aggression towards cubs is well known in present-day bears (McCullough, 1981; Tietje *et al.*, 1986; LeCount, 1987; Miller, 1990; Craighead *et al.*, 1995; Derocher & Wiig, 1999). Bears hibernate in their second winter for the first time (Craighead *et al.*, 1995; McNamee, 1997). Difficulties in establishing and maintaining special

metabolic processes that are characteristic of hibernation (Nelson *et al.*, 1983; Hellgren, 1998) could be important factor for the observed high mortality during this period. When their fat reserves are not adequate, bears are unable to start hibernating, however, only hibernation enables them to survive more than 6 months without food. Cases of yearlings that died in their den during especially long winters have been reported for present-day bears (Schoen *et al.*, 1987; Rogers, 1981; 1987).

The frequency of 2-year-old individuals is also high, but significantly lower than in yearlings (Fig. 3), which indicates a sharp decline in mortality after the second winter. The proportion of yearlings in comparison to 2-year-olds was presumably even larger originally, because their teeth were much more prone to destruction. M_1 teeth of yearlings have only about 1.25 mm thick root wall and are therefore more easily fragmented than M_1 teeth of 2-year-old individuals with mechanically more resistant, approximately 2.5 mm thick root wall.

The measurements of thickness of root wall by juve-

nile M_1 teeth (Fig. 5) yielded another conclusion, that the mortality in the cave was not distributed evenly throughout the year. The first peak in the distribution shown in Fig. 5 represents yearlings that died during their second winter or in the following early spring. The second peak consists of 2-year-olds that died in their third winter. The intervening hiatus indicates that bears were absent from the cave during the second summer period. Specimens that could be attributed to about 6-8-month-old cubs are also missing in the sample. Both gaps in the mortality profile suggest that cave bears were not returning to the cave after they had left it in the spring (from April to early June). Perhaps they visited it occasionally, but they stayed away at least during months of intensive feeding. Microscopic analysis of growth layers in dental tissues (dentine and cementum) has also shown that great majority of deaths in the Mokrica cave occurred during the hibernation and in a short post-hibernation period. The same results from Potočka zijalka (Debeljak, 2004) contradict some older assumptions that high Alpine caves were continuously occupied by bears in all seasons, all the year round (Ehrenberg & Sickenberg, 1929; Ehrenberg, 1967).

It seems that mortality of 3-year-olds was not much lower than in 2-year-olds (Fig. 3). Although 3-year-olds were physically stronger, this was probably quite a critical age. Brown bear females usually abandon their young at the age of about 2.5 years, sometimes one year earlier or later (Bunnell & Tait, 1981; Craighead *et al.*, 1995). Prominent decline of mortality by 4-year-olds (Fig. 3) indicates that the weaning period presumably took place already in the third year, like in present-day bears.

Frequencies of M_1 teeth belonging to young adults are more or less evenly distributed through one-year intervals (Fig. 3). At the age of 5-8 years brown bear females wean their young for the first time (Bunnell & Tait, 1981; Craighead *et al.*, 1995). The mortality could be somewhat higher in young, inexperienced cave bear females in comparison to older females. Fig. 3 shows that there was a further decline of mortality by prime adults, after the age of 8, and became more prominent again after the age of 15. As in present-day bears, the mortality caused by factors other than man is extremely low in this age group (McNamee, 1997). Rare cases of 9-15-year-old bears that died in the Mokrica cave could be explained by natural causes (injuries, disease) and perhaps even by occasional hunting by prehistoric man. Rakovec (1967) assumed that man came to the cave from time to time only, above all during the summer months when he hunted cave bears. However, there is no direct evidence for cave bear hunting in the Mokrica cave. Furthermore, the supposed hunting would probably take place during hibernation, when bears were in the most vulnerable position.

It seems that in the group of older adults, mortality

started to rise already at the age of 16 (Fig. 3). In Potočka zijalka moderate mortality increase was observed not earlier than around the age of 20. This difference could be due to a small sample size. The proportion of individuals older than 20 years was most likely higher in the original death assemblage than it could be inferred from the analysed sample (Fig. 3), because remnants of extremely worn teeth were easily broken and have not been recovered during excavations. There is a somewhat lower proportion of older adults in the sample of isolated M_1 teeth (Fig. 3) than in the sample of all M_1 teeth (Figs. 4 and 5), because 12 out of 21 M_1 specimens still firmly attached in the mandibles were attributed to individuals older than 15 years, based on their crown wear. However, without sectioning the root and microscopic examination of dental cementum it was not possible to accurately determine their individual age.

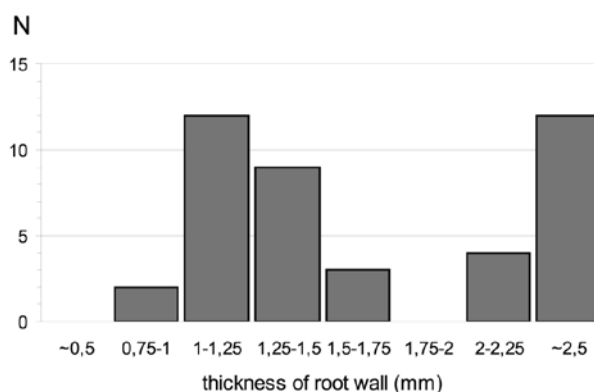


Fig. 5: Number of M_1 specimens in classes with particular thickness of root wall, measured approximately 7.5 mm under the crown. Specimens ($N=42$) belonged to yearlings and 2-year-olds.

Mortality around the age of 20 can be attributed to senescence-related malnutrition and disease. M_1 teeth were heavily worn by this age, sometimes to such a degree that pulp canal in the root became exposed. Dental pathologies are very frequent on jawbones of older cave bears, that could hinder feeding to such degree that animal could not gain enough weight before winter. It has been suggested in the past that the longevity in cave bear was severely restricted by the heavy wear of teeth and that it was somewhat shorter than in the brown bear, because cave bear teeth wore out more quickly. Kurtén (1958; 1976) expressed doubt that any cave bear lived beyond about twenty years of age. The mortality profile from the Mokrica cave does not support this hypothesis. The oldest age recorded is approximately 30 years, which indicates that the maximum life span was similar to present-day bears; in the wild their life span is 25-30 years (Bunnell & Tait, 1981; Derocher, 2000).

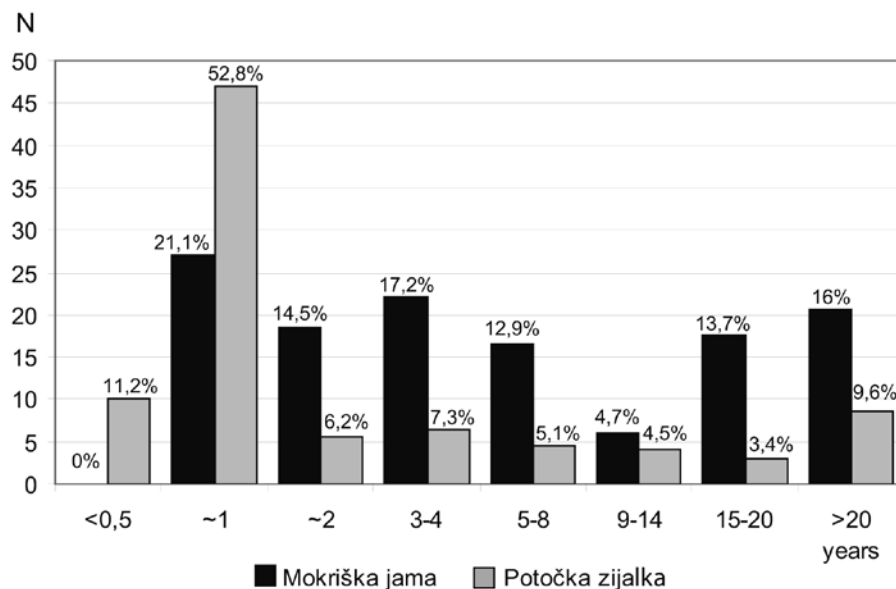


Fig. 6: Frequencies and percentages of left lower M_1 teeth in different age classes from Mokriška jama ($N=128$) and Potočka zijalka ($N=89$).

The comparison of proportions of different age groups for the Mokrica cave and Potočka zijalka is given in Fig. 6. The most striking difference between the two sites is in the proportion of individuals younger than 18 months, which is much higher in Potočka zijalka (64% vs. 21.1% in the Mokrica cave). Such a discrepancy could be at least theoretically explained if Potočka zijalka cave would be used primarily by females and their offspring and the Mokrica cave on the other hand by adult males. However, this was obviously not the case. On the contrary, males predominate in Potočka zijalka in even higher proportion than in the Mokrica cave. It is also not likely that different ecological conditions would influence the survival rate of juveniles to such a great degree. As it has been already pointed out, teeth of individuals younger than 18 months are hollow and were therefore much more prone to destruction than teeth of older individuals. In the analysed sample of 89 M_1 teeth from Potočka zijalka, there are even 10 specimens (11.2%) of 2-4-month-old individuals, which indicates the exceptionally good state of preservation of the fossil material. This assumption is further supported by the very high ratio of M_1 teeth of yearlings to mechanically more resistant M_1 teeth of 2-year-olds; the ratio of 8.5 to 1 has been established in the Potočka zijalka sample, in comparison to less than 1.5 to 1 ratio for the Mokrica cave. Teeth and mandibles from Potočka zijalka are generally in a much better state of preservation than those from the Mokrica cave. Discrepancy in the proportion of less than 18 month old individuals between the two sites could be therefore explained by different taphonomic conditions. Sediment

protects skeletal material from destructive taphonomic factors, such as scavenging, trampling and weathering (Lyman, 1994). The conditions were more favourable for preservation of juvenile teeth when the material became quickly buried in the sediment, which was probably the case in Potočka zijalka. Furthermore, the proportion of hollow and for this reason often fragmented juvenile teeth is also related to the accuracy in collecting fossil material during excavations. In Potočka zijalka also fragmented teeth were recovered during the new 1997-2000 excavation campaign (Pacher *et al.*, 2004). On the other hand, only more or less

complete teeth were kept in the more than 50 year old collection of cave bear material from the Mokrica cave. This could additionally contribute to the underrepresentation of juvenile specimens in the analysed sample. If we exclude M_1 specimens of less than 18 month old individuals, that are most sensitive to different taphonomic conditions and recovery techniques, we get very similar proportions of the remaining age groups for both sites: there are 40.1% of 2-4-year-olds, 39.6% of young- and prime adults, and 20.3% of more than 20 years old adults in the Mokrica sample ($n=101$), and 37.5% of 2-4-year-olds, 35.9% of young- and prime adults, and 26.6% of old adults in the Potočka zijalka sample ($n=32$).

After the model proposed by Stiner (1990; 1994; 1998), the fossil population from the Mokrica cave exhibits the so-called 'normal non-violent attrition' (NNVA) mortality pattern, which is in Stiner's opinion consistent with hibernation-related mortality, caused by non-violent factors, principally starvation. However, in Potočka zijalka, where fossil material is better preserved, 'juvenile-dominated' mortality pattern has been established (Fig. 7). Considering the presumed underrepresentation of juveniles in the analysed sample, the original death assemblage was most likely distinctly juvenile-dominated in the Mokrica cave as well. The predominance of juveniles has been reported from many cave bear sites (Bächler, 1957; Kurtén, 1958; Rabeder, 1992; Andrews & Turner, 1992; Grandal d'Anglade & Vidal Romani, 1997; Weinstock, 1999; 2000; 2001; Pacher, 2000; Germonpré & Sablin, 2001; Debeljak, 2002; Turner, 2002). In my opin-

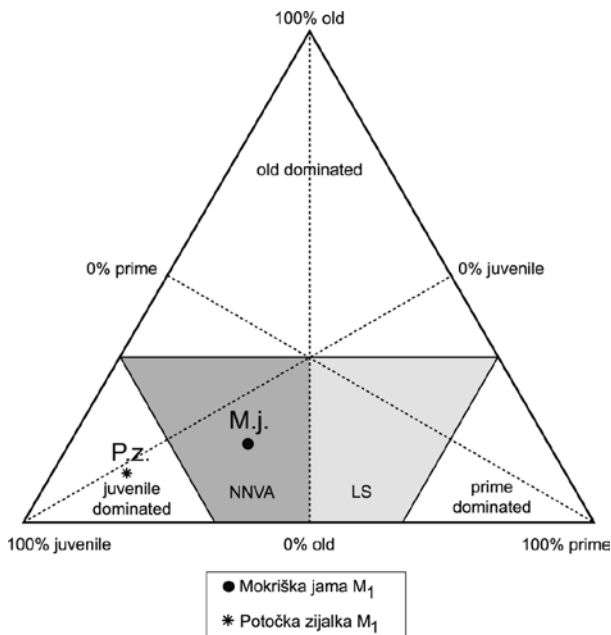


Fig. 7: Tripolar graph denoting proportions of three main age categories in the samples of left M_1 teeth from the Mokrica cave and Potočka zijalka. After Stiner (1990; 1994; 1998) – dark grey field represents NNVA (normal non-violent attrition) mortality pattern and light grey LS (living structure) pattern.

ion, the juvenile-dominated population structure is characteristic of hibernation-related mortality in typical cave bear sites, provided that fossil material, including fragile juvenile teeth, is well preserved and accurately collected. Mortality patterns in the Mokrica cave and Potočka zijalka show no evidence for intensive, non-selective cave bear hunting, which should, according to Stiner (1990; 1994; 1998), affect all age groups randomly and result in

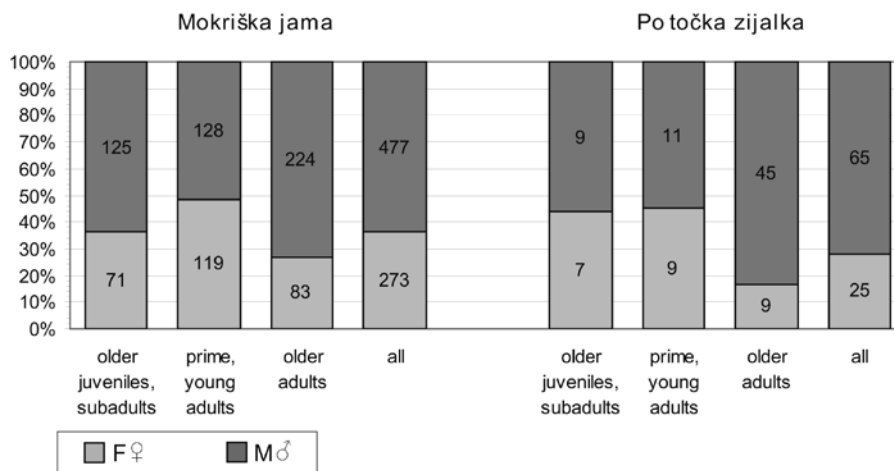


Fig. 8: The proportion of female canines to male canines (upper and lower) in different age groups for the Mokrica cave ($N=750$) and Potočka zijalka ($N=90$). Number of specimens is shown inside the bars.

the so-called 'living structure' (LS) mortality pattern, resembling the age structure of the living population.

SEX STRUCTURE:

The results of sexing 750 canines of individuals older than 18 months are presented in Fig. 8. In the group of older juveniles (2-year-olds) and subadults (3-4-year-olds), males predominate over females with 1.8 to 1 ratio (63.8% males, 36.2% females). This could be explained with higher mortality rate of males in this age class, which was observed also in populations of present-day bears. The weaning period is obviously somewhat more critical for males than females. Subadult females are better tolerated by adult females and are often allowed to stay in the same home range after weaning, while subadult males usually travel larger distances to establish their own territory (Elowe & Dodge, 1989; Swenson *et al.*, 1998; McLellan & Hovey, 2001). They can be outcompeted in the search for food and can fall prey to adult males, who can be very aggressive toward subadult males. Intraspecific competition is especially enhanced by high population density and shortage of available food (McCullough, 1981; Bunnell & Tait, 1981; Tietje *et al.*, 1986; McNamee, 1997).

The proportion of males and females is nearly equal in the group of young and prime adults (~5-15-year-olds). Hibernation period is considerably prolonged in females with cubs in comparison to solitary males in present-day bears (Judd *et al.*, 1986; Schoen *et al.*, 1987; Schwartz *et al.*, 1987; Miller, 1990; Van Daele *et al.*, 1990; McNamee, 1997; Manchi & Swenson, 2005). Furthermore, females can get injured when protecting their offspring. We assume that mortality was actually somewhat higher in adult females than in adult males. However, if solitary males dened in the Mokrica cave more frequently, this

could result in approximately equal proportion of both sexes in the fossil population. In present day bears, females first produce cubs by the age of 5-8 years (Bunnell & Tait, 1981; Craighead *et al.*, 1995). In the sample of 247 canines of prime and young adults, 42 specimens belong to the 5-8 years age class. Interestingly, 28 of them are of females and only 14 of males (2:1 ratio). It should be taken into consideration that large, unworn canines are the most attractive finds and that males could be artificially underrepresented in this age group. If not, this

could be the evidence that maternity-related mortality was increased especially in the group of very young, inexperienced females.

In the group of older adults (~ 15-25-year-olds) males considerably outnumber females (73% males, 27% females; 2.7:1 ratio), which is another indication that the Mokrica cave was mostly occupied by solitary males. Old females obviously chose the cave for their denning place

less often. In Potočka zijalka, even higher proportion of males (83.3%) is observed in this age class. The predominance of males cannot be explained by the assumption that males lived longer on average than females. This is not the case in present-day bears. On the contrary, some data even show that females live longer on average than males (Craighead *et al.*, 1995; McNamee, 1997; Wiig, 2000).

CONCLUSIONS

Mortality pattern in the Mokrica cave shows no evidence for intensive, non-selective cave bear hunting. The age structure of the analysed sample of the cave bear fossil population exhibits the so-called 'normal non-violent attrition' (NNVA) mortality pattern, with a 52.7% share of juveniles and subadults (1-4-year-olds), 31.3% of young- and prime adults (5-20-year olds) and 16% of old adults (>20 years old individuals). The Mokrica cave was used by cave bears as a winter and birthing den and was presumably not visited regularly during summer months. The majority of deaths occurred during hibernation or in short posthibernation period, mainly because of starvation and predator attacks. Mortality was presumably highest in the first winter when cubs were born, however, extremely fragile crowns of M_1 teeth of individuals younger than 4 months have not been preserved. Yearlings (9-15-month-old individuals) are the largest age class with 21.1% share. Hollow teeth of yearlings presumably underwent much higher taphonomic losses than mechanically more resistant teeth of older individuals. It can be inferred that the proportion of individuals younger than 18 months was much higher originally and that the death assemblage was markedly 'juvenile-dominated'. The mortality rate dropped drastically after cave bears successfully survived the second winter. The next signifi-

cant decrease of mortality occurred at the age of 4 years, which indicates that females left their young in the third year on average, like in present-day bears. The weaning age is especially critical for subadult males, which could explain higher proportion of males (63.8% M, 36.2% F) in the group of older juveniles and subadults.

The mortality rate in young adults (5-8-year-olds) was still much higher than in prime adults. From the age of 9 to 15 years, deaths were very rare. Mortality was presumably higher in females, because they hibernated longer than males. However, solitary males probably denned in the Mokrica cave more frequently, which resulted in approximately equal proportion of both sexes (51.8% M, 48.2% F) in the studied sample of canines of young- and prime adults (5-15-year-olds). In the sample of older adults, however, males clearly predominate (73% M, 27% F), which is another indication that the Mokrica cave was mostly occupied by solitary males. Old females chose the cave for their denning place less often. Moderate increase in mortality can be observed already after the age of 16. Mortality around the age of 20 can be attributed to senescence-related malnutrition and disease. The oldest age recorded by cementum analysis is approximately 30 years, which indicates that the maximum life span was similar as in present-day bears.

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