

The Age and Sex Structure of the Cave Bear Population from Križna jama (Slovenia)

by

Irena Debeljak ¹⁾

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Zusammenfassung

Für 28 Höhlenbären, die in der Križna jama gestorben sind, wurde das Sterbealter auf der Basis aller d_4 und M_1 bestimmt. Das Ergebnis zeigt einen vergleichsweise geringen Anteil an Jungtieren (32,1%) und einen relativ großen Anteil (28,6%) an senilen Individuen. Die Anwesenheit von Jungen unter einem Alter von drei Monaten zeigt, dass die Bärinnen die Križna jama auch als Wochenstube gebraucht haben um ihre Jungen zur Zeit des Winterschlafes zur Welt zu bringen. Das höchste, durch Zählung der Zementanwachslinien bestimmte Alter wies ein seniles Männchen auf, das 28 Jahre erreichte. Das zeigt, dass die Lebensspanne des Höhlenbären in etwa der des rezenten Braunbären entsprochen hat.

Die Bestimmung der Jahreszeit zum Todeseintritt wurde für 10 jüngere Individuen anhand der Zahnentwicklung und der letzten Zementanwachslinie durchgeführt. Die Mehrzahl der Todesfälle ist im Winter, also während der Zeit der Überwinterung, eingetreten. Es besteht auch die Möglichkeit, dass einige Bären die Höhle auch vor oder nach der Überwinterung aufgesucht haben und dabei gestorben sind. Die Geschlechterverhältnis wurde anhand von 67 Eckzähnen von Bären – die älter als 18 Monate waren – bestimmt. Mehr als 73% der Bären waren Männchen, das Verhältnis von Männchen zu Weibchen beträgt somit 2,72. Das zeigt, dass die Križna jama vor allem von adulten und senilen männlichen Bären zur Überwinterung genutzt wurde.

Schlüsselwörter: Križna jama, Höhlenbären, Zähne, Zahnzementanwachslinien, Bestimmung des individuellen Alters, Bestimmung der Jahreszeit beim Todeseintritt, Sex-Struktur

Abstract

The age of 28 individual cave bears that died in Križna jama has been determined by the analysis of all left specimens of d_4 milk teeth and M_1 permanent teeth. The results show a relatively low proportion of juveniles (32.1%) and a large proportion of old animals (28.6%). The presence of individuals younger than 3 months indicates that females gave birth to cubs in Križna jama during hibernation. The oldest age was reached by a large male that lived for about 28 years, which was determined by counting cementum increments. The life span of the cave bear was therefore similar to that of the modern brown bear. Season at the time of death has been estimated for 10 younger individuals by the analysis of tooth development and by examining the last cementum increment. The majority of deaths occurred in winter, during denning. It is possible, however, that some bears died in the cave before and shortly after the hibernation period. Sex structure has been studied on the sample of 67 canines of individuals older than 18 months. More than 73% of them belonged to males, which gives a male to female ratio of 2.72. It can be assumed that Križna jama was used as a winter den mostly by prime adult and old male bears.

Keywords: Križna jama, cave bear, teeth, cementum increments, individual age determination, season at death, sex structure

Izvilleček

Na podlagi analize vseh levih primerkov mlečnih d_4 zob in stalnih M_1 zob je bila določena individualna starost 28 različnih osebkov jamskega medveda, ki so poginili v Križni jami. Rezultati kažejo relativno nizek delež mladičev (32,1%) in velik delež starih živali (28,6%). Prisotnost manj kot 3 mesece starih osebkov dokazuje, da so samice v Križni jami med hibernacijo kotile mladiče. Najvišjo starost je dosegel velik samec, ki je živel približno 28 let, kar je bilo ugotovljeno s štetjem cementnih pri-rastnic. Življenjska doba jamskih medvedov je bila torej

¹⁾ Dr. Irena DEBELJAK, Ivan Rakovec Institute of Palaeontology, ZRC SAZU, Novi trg 2, Ljubljana, Slovenia, e-mail: IrenaDe@zrc-sazu.si

približno tako dolga kot pri današnjih rjavih medvedih. Za 10 mlajših osebkov je bilo mogoče oceniti sezono ob smrti, in sicer po analizi razvitosti zob ter s preiskavo zadnje cementne prirastnice. Večina živali je poginila pozimi. Možno pa je tudi, da so nekateri medvedi v jami poginili tudi že pred hibernacijo in v kratkem obdobju po hibernaciji. Spolna struktura je bila proučena na vzorcu 67 podočnikov več kot poldrugo leto starih osebkov. Od teh jih je več kot 73% pripadalo samcem, tako da razmerje samcev proti samicam znaša 2,72. Sklepamo lahko, da so Križno jamo kot zimski brlog večinoma uporabljali zreli odrasli in stari samci.

Ključne besede: Križna jama, jamski medved, zobje, cementne prirastnice, določanje individualne starosti, sezona smrti, spolna struktura

1. Introduction

The aim of this study was to determine the sex, individual age, and season at the time of death of cave bears from Križna jama. The studied material was found during excavations in 1999 and 2001 conducted by Prof. Vida Pohar (University of Ljubljana, Slovenia) and Prof. Gernot Rabeder (University of Vienna, Austria). This study is a part of the broad-based, still ongoing research concerning the structure of cave bear populations from different Slovenian sites (DEBELJAK, 2002; 2004; 2007; 2011) with the purpose of acquiring new data on the biology, behaviour, ecology, and mortality of this extinct species. Križna jama is of special interest here because it represents a much larger and more complex cave system than the other Slovenian sites containing cave bear remains which have been examined thus far.

Križna jama is a more than 8 km long underground river cave, located in the karstic Notranjska region, north of the town Lož (SW Slovenia). Its altitude at the entrance is about 630 metres above sea level. Cave bear remains included in this study are of Middle Würmian age. Radiocarbon dating results constrain their ages between 47.000 and 32.000 years BP (RABEDER & WITHALM, 2001; POHAR et al. 2002; RABEDER, 2009; BOSÁK et al., 2010; RABEDER et al., this volume). Cave bears from Križna jama are particularly large and belong to the highly evolved *Ursus ingressus* lineage (RABEDER & HOFREITER, 2004; RABEDER, 2009; this volume).

2. Sex Structure

Due to pronounced sexual dimorphism, a cave bear's sex can be determined from the dimensions of the canines (KOBY, 1949; KURTÉN, 1955). Thus, the sex ratio, i.e. the ratio of males to females in a cave bear site, can be estimated from the sample of all canines (isolated or still attached to the jawbones) of individuals older than 18 months. Canines of individuals less than 18 months old are unerupted teeth with no root, consisting only of a hollow crown, which is often damaged at the base and difficult to measure reliably. For this reason the canines of yearlings were not included in the analysed sample. The dimensions of upper and lower canines do not differ significantly and can be analysed together.

The results of measurements of the crown width (i.e. transverse diameter) of 44 well-preserved canines from Križna jama are presented in a histogram in Figure 1. As expected, there is clear bimodal distribution which allows us to reliably separate canines of males and females.

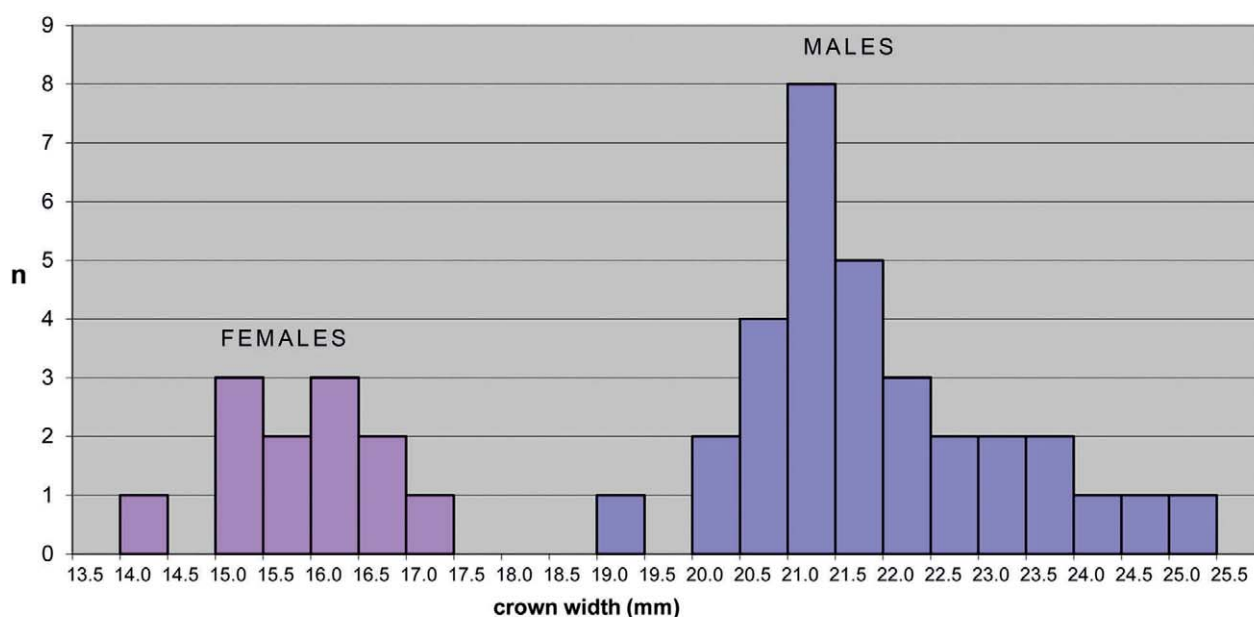


Figure 1: Histogram of the crown width of upper and lower canines (44 specimens) from Križna jama. Bimodal distribution indicates pronounced sexual dimorphism.

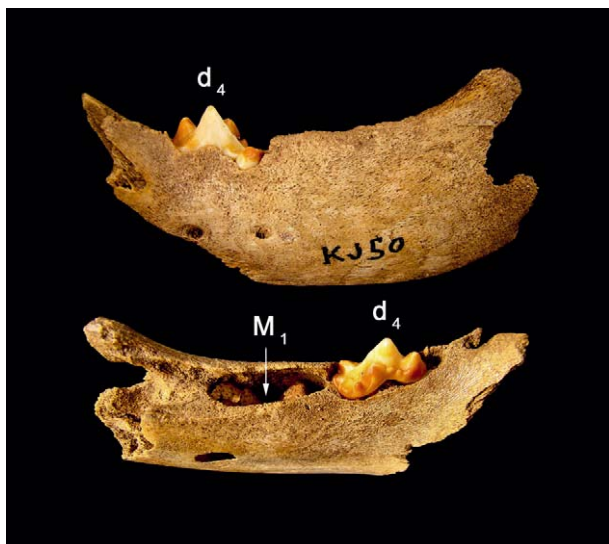


Figure 2: Left mandible (KJ 50) of a 2–3 month old cub from Križna jama. D_4 milk tooth is not fully erupted. The crown of permanent M_1 tooth is still completely encased in the jawbone. Buccal and linguo-occlusal views. Natural size.

The size difference between male and female canines is so obvious that sex can be identified from their overall dimensions, usually also in the case of specimens that are too worn or too damaged to be measured accurately. In this way, sex was determined for 67 canines altogether. Forty-nine of them (73.1%) belonged to males and only 18 (26.9%) to females. Male to female ratio is 2.72 – the cave bear population from Križna jama is therefore highly dominated by males. The same conclusion was drawn by RABEDER & WITHALM (this volume). The prevalence of males in Križna jama is not surprising. It supports the assumption of KURTÉN (1955) that large caves were chosen for denning mostly by males, whereas females preferred small caves with hidden entrances allowing them to protect their cubs from adult males.

Interestingly, the predominance of males is particularly pronounced in the group of canines with their root still widely open at the apex, that belonged to 2–4 year old animals, i.e. older juveniles and subadults. In the sample of 9 specimens, 8 belonged to males and only one to a female, which could indicate a higher mortality of males in this age group. A similar situation was observed in the sex structure of cave bear population from Mokriška jama (DEBELJAK, 2007). Also in modern bears, the age period of 2–4 years is more critical for males than females. Cubs are usually weaned at the age of two or three years, when their mothers chase them away or abandon them. 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 large distances to find their own territory (ELOWE & DODGE, 1989; SWENSON et al., 1998; McLELLAN & HOVEY, 2001). They can be overcompeted in the search for food or fall prey to adult males, who can be very aggressive towards

subadult males. Intraspecific competition is enhanced by high population density and in case of shortage of available food (McCULLOUGH, 1981; BUNNEL & TAIT, 1981; TIETJE et al., 1986; McNAMEE, 1997).

3. The Youngest Cubs

Neonates, i.e. infants that died in the first month after birth, cannot be studied on the basis of their teeth. Milk teeth developed to a sufficient degree and started to erupt only in the second or third month of life (DEBELJAK, 1997). Cubs that died at the age of 1–6 months are best represented by d_4 teeth, which are the largest milk teeth. Nevertheless, they are still quite small (Fig. 2) and usually overlooked during excavations if the sediment is not water-sieved. So far, only excavations in Divje babe I cave have yielded a considerably large sample. In the study of the Divje babe population structure, more than 900 specimens of left d_4 teeth were analysed (DEBELJAK, 2002). From Križna jama, however, only 5 specimens of left d_4 teeth (4 isolated and 1 in mandible) were available for the analysis (Table 1). The roots of three of them were completely resorbed – they were probably shed naturally during denning in the second winter. Therefore, they do not represent dead individuals. The remaining two specimens belonged to 2–3 month old cubs, which is another piece of evidence that females occasionally gave birth to cubs in Križna jama, although it was mostly occupied by adult males. Considering the fact that bears are usually born in January, these two cubs probably died in March or April, a month or two before they would have left the winter den with their mother. Possible causes of their death could have been disease or maternal abandonment, as observed in modern bears (ELOWE & DODGE, 1989). Furthermore, they could have been killed by predators, or even more likely by an adult male cave bear. In all bear species, males practice infanticide either to make the female sexually receptive or simply for the purpose of consumption (McCULLOUGH, 1981; TIETJE et al., 1986; LECOUNT, 1987; MILLER, 1990; CRAIGHEAD et al., 1995; DEROCHER & WIIG, 1999; WITTENBERG & WENDZELIDES, 2000).

A well preserved mandible (KJ 50) of approximately 2 month old cub from Križna jama with the erupting d_4 tooth is shown in Figure 2. Individual age was determined by using data concerning the ontogenetic development of teeth in different bear species (POHLE, 1923; DITTRICH, 1960; MARKS & ERICKSON, 1966; DEBELJAK, 1997).

4. Yearlings and 2-year-olds

Individuals older than 6 months are usually best represented by M_1 teeth, which are the first permanent teeth to develop and erupt in bears (DITTRICH, 1960). As in the other Slovenian localities, left lower M_1 teeth were chosen for the study of age structure of the cave bear population from Križna jama. In the sample of 26 left M_1

teeth, 7 specimens belonged to yearlings and 2-year-olds (Table 1). The thickness of their root wall was measured in cross sections about 7 mm below the crown, as shown in Figure 3. Furthermore, the relative width of the anterior and posterior root canal was determined for each specimen (Table 1: r. ant., r. post.). It is defined as the diameter of the tooth root divided by the diameter of the root canal (Fig. 3: AB/CD). In juveniles, all data of this sort can be used as a criterion to assess individual age and season at the time of death (DEBELJAK, 2002; 2004; 2007; 2011). M_1 teeth erupted during the first summer at the age of about 5 months. Initially, the teeth were completely hollow, then gradually became filled with secondary dentin during the first four years of life, until only a narrow canal remained in the centre of their roots (see e.g. DEBELJAK, 2011, Plate 1, Figs. 2a–c, 3a). For comparison: M_1 root wall is about 1.25 mm thick in yearlings, and 2.5 mm thick in 2-year-olds. Interestingly, in a large sample of M_1 teeth from Divje babe I, Mokriška jama, Potočka zijalka and Ajdovska jama, there are very few specimens with 1.75–2.25 mm thick root wall, because at this stage of ontogenetic development, bears were usually absent from the caves. In Križna jama, however, 4 such specimens were found, which is a large number, considering the small sample size.

This unusual situation is clearly observable in the scatter plot of relative width of anterior and posterior root canal in M_1 teeth from different Slovenian cave bear sites (Fig. 4). Specimens from Križna jama are marked with red dots. A circle shows the approximate position of two broken specimens (KJ 50a and KJ 51) where only a single root canal could be measured (Table 1). The group of yearlings (black dots) is clearly separated from the group of 2-year-olds (grey dots) by a prominent gap in distribution. This proves that the mortality was not distributed evenly throughout the year. The vast majority of bears, whose remains have been recovered from Divje babe I, Mokriška jama, Potočka zijalka, and Ajdovska jama, died during the denning period, from October to May or June.

At the height of the summer season, on the other hand, there was literally no mortality. The four specimens from Križna jama mentioned above belong to the upper range of yearlings and the lowermost range of 2-year olds, and there is another specimen in the lowermost range of yearlings. This could indicate that cave bears stayed in Križna jama somewhat longer in the spring and started denning somewhat earlier than average. However, the analysed sample is too small to allow us to draw any reliable conclusions of this sort. Determination of the season at the time death by dental cementum analysis, which will be described below, is unfortunately very difficult to apply in the case of animals younger than 2 years. The results are not completely reliable, but it seems quite possible that the two yearlings, marked as KJ 184a and KJ 6, died already in the post-hibernation period and that specimen KJ 50a belonged to a less than 2 year old juvenile that died before the beginning of hibernation (Table 1).

Like in the previous age group, possible causes of death in 1–2 year old juveniles could be adult male aggression, attacks by lions, hyenas, or wolf packs, premature maternal abandonment, and malnutrition. When their fat reserves are not adequate, bears are unable to survive 6 or more months without food. Cases of yearlings dying in their den during particularly long winters have also been reported for modern bears (SCHOEN et al., 1987; ROGERS, 1981; 1987).

5. Subadults and Prime Adults

In subadult and adult bears, individual age can be determined by counting dental cementum increments. This is the most reliable and objective method that has long been used routinely in modern bears, as well (RAUSCH, 1961; MUNDY & FULLER, 1964; MARKS & ERICKSON, 1966; HENSEL & SORENSON, 1980; HARSHYNE et al., 1998; CALVERT & RAMSAY, 1998). Cementum is bone-like tissue that is continuously deposited on the surface

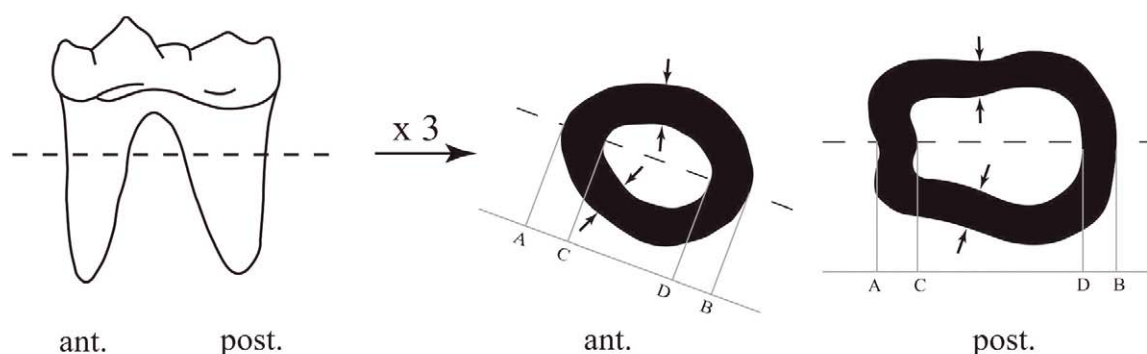


Figure 3: Sketch of M_1 tooth in natural size, and magnified cross section through the anterior and posterior root at the age of 1 year. Arrows indicate where the thickness of root wall can be measured. AB: diameter of root, CD: diameter of root canal.

LEFT LOWER D ₄ :						
Inv. no.	Description	Stage	Individual age	Season at death		
mand. KJ 50	erupting	1-2	2 months	„winter“		
KJ 51	slightly open root apices	2	2-3 months	„winter“		
KJ 54	resorbed root – shed milk tooth	6				
KJ 62	resorbed root – shed milk tooth	6				
KJ 185	resorbed root – shed milk tooth	6				
LEFT LOWER M ₁ :						
Inv. no.	Length (mm)	Width (mm)	Root wall (mm)	R. ant.	R. post.	Season at death
KJ 12a	30.7	15.8	0.75-1		1.22	1 year early „winter“
KJ 118	27.6	13.4	1-1.25	1.46	1.32	1 year „winter“
KJ 184a	32.5	15.7	1.75-2	1.72	1.45	1-1.5 years late „winter“ – early „summer“
KJ 6	28.7	13.9	1.75-2	1.74	1.48	1-1.5 years late „winter“ – early „summer“
KJ 50a		14.3	2-2.25		1.66	1.5-2 years late „summer“ – early „winter“
KJ 51			2-2.25	1.98		2 years early „winter“
KJ 12b			~ 2.5			2 years
KJ 50/1	31.7	16.0	~ 3	4.13	2.99	3 years early „winter“
KJ 184b	29.6	14.3	~ 3.5	5.20	3.75	3-4 years
KJ 145	29.3	14.2				8 years „winter“
KJ 50/4						13-15 years
KJ 50/3	~ 31.2	15.6				16-18 years
KJ 62	~ 29.3	~ 14.4				17-19 years
KJ 11/1	~ 32.7	~ 16.5				18-20 years
KJ 168	~ 29.8	~ 14.5				18-20 years
KJ 210		~ 14.5				20-22 years
KJ 50b						20-22 years
KJ 134	~ 29.1	~ 14.1				22-24 years
KJ 146	~ 29.1	~ 14.2				23-25 years
KJ 50/5	~ 29.3	~ 14.6				24-26 years
KJ 11	~ 30.0	~ 14.4				24-26 years
KJ 119	~ 32.9	~ 16.9				26-30 years
mand. KJ 89						~ 10 years
mand. KJ						~ 10 years
mand. KJ 231						~ 10-15 years
mand. KJ 001						~ 25 years

Table 1: Individual age estimations and other data for left lower d₄ teeth (5 specimens: 4 isolated, 1 in mandible) and left lower M₁ teeth (26 specimens: 22 isolated, 4 in mandible) from Križna jama. „Winter“ season is the period when bears stayed in their winter den – from late autumn to early spring. The remainder of the year is considered as „summer“.

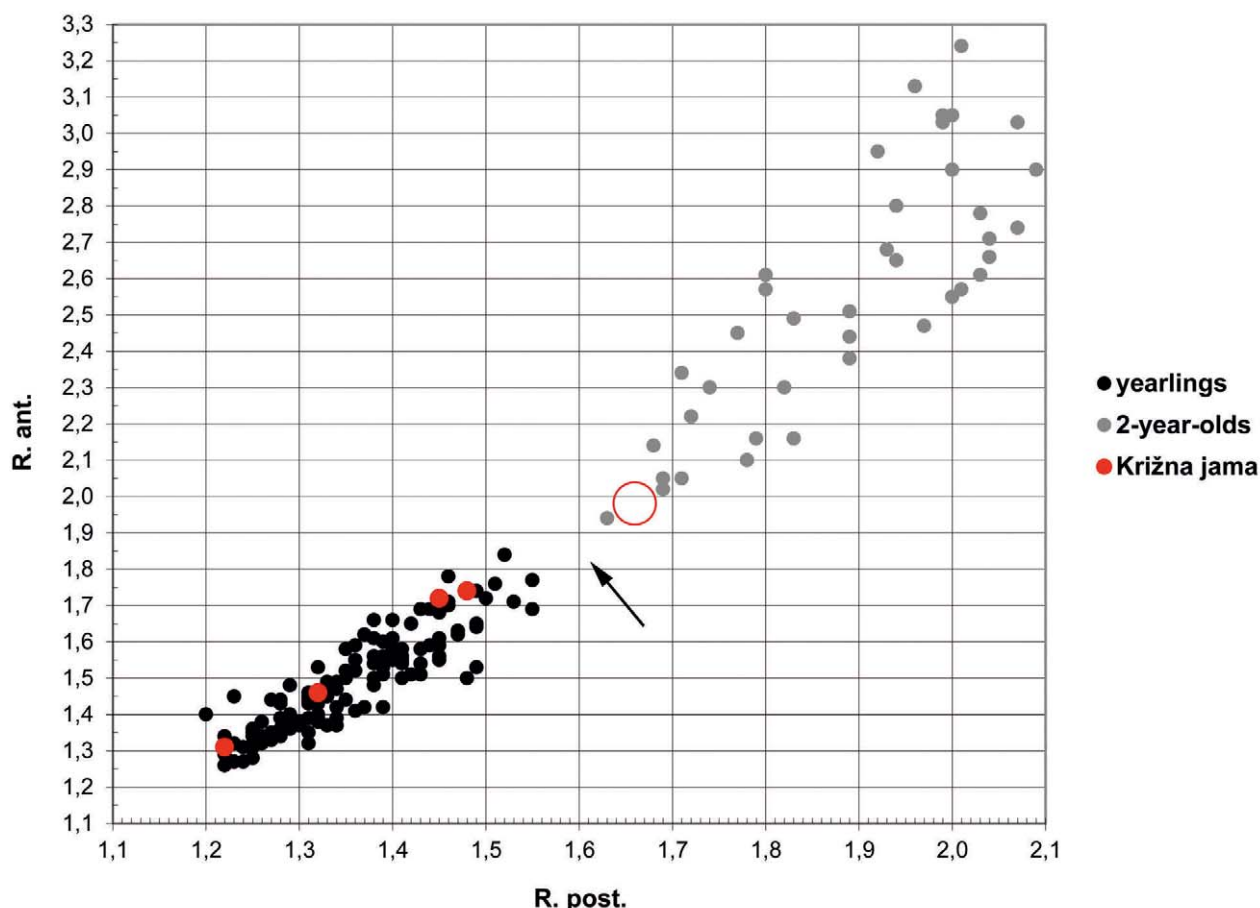


Figure 4: Scatter plot of the relative width of pulp canal in the posterior and anterior root (r. post., r. ant.) showing the degree of root development in M_1 teeth of yearlings (black dots) and 2-year-olds (grey dots) from different Slovenian sites (Divje babe I, Mokriška jama, Potočka zijalka, and Ajdovska jama). Four specimens of yearlings from Križna jama are marked with red dots. Red circle indicates the approximate position of two Križna jama specimens in which only the anterior or posterior root is preserved. An arrow points to hiatus in distribution.

of tooth roots throughout the entire life. It is composed of the so-called „winter“ and „summer“ layers, similar to growth rings in trees. The first 5–8 annuli are generally much wider than the rest (Fig. 5). Season at the time of death can be estimated in well-preserved specimens of subadults and younger adults by examining the last (outermost) cementum increment. In a 3-year old specimen depicted in Figure 6, for example, a dark „winter“ increment just started to form, indicating that death occurred early in the denning period. In bears older than about 8 years, however, season at death usually cannot be determined, because of progressively thinner and tightly packed cementum increments. No „summer“ and „winter“ increments can be distinguished in cementum at an older age, only fine reversal lines between annual layers, that enable us to estimate individual age in years (for more details see DEBELJAK, 2011).

Dental cementum has been examined in all 22 isolated specimens of left M_1 teeth from Križna jama. For this purpose, tooth roots were cut transversely about 7 mm below the crown. Thin sections and etched/coloured

ground sections were prepared as described by DEBELJAK (1996; 2000). Ground sections were etched with 10–12% orthophosphoric acid (H_3PO_4) for 3–5 minutes, and then coloured with approximately 0.5% aqueous solution of gentian violet. During this process tooth crowns were always left intact. The teeth still attached in mandibles were not cut, and their cementum was not examined, because it would be impossible to extract them without damaging the jawbone. Individual age was roughly estimated for 4 such specimens by comparing their crown wear patterns to the teeth of known individual age.

Individual age estimations and other collected data for all studied specimens are presented in Table 1. Measurements of crown length and width were taken when possible. Furthermore, occlusal wear was recorded according to the scheme of nine stages (I–IX) proposed by STINER (1994; 1998). Two M_1 specimens out of 26 belonged to 3–4 year old immature bears (subadults), that probably already lost the company and protection of their mothers. As discussed in Section 2, bears, especially males, are very vulnerable at this age. Brown bear females usually

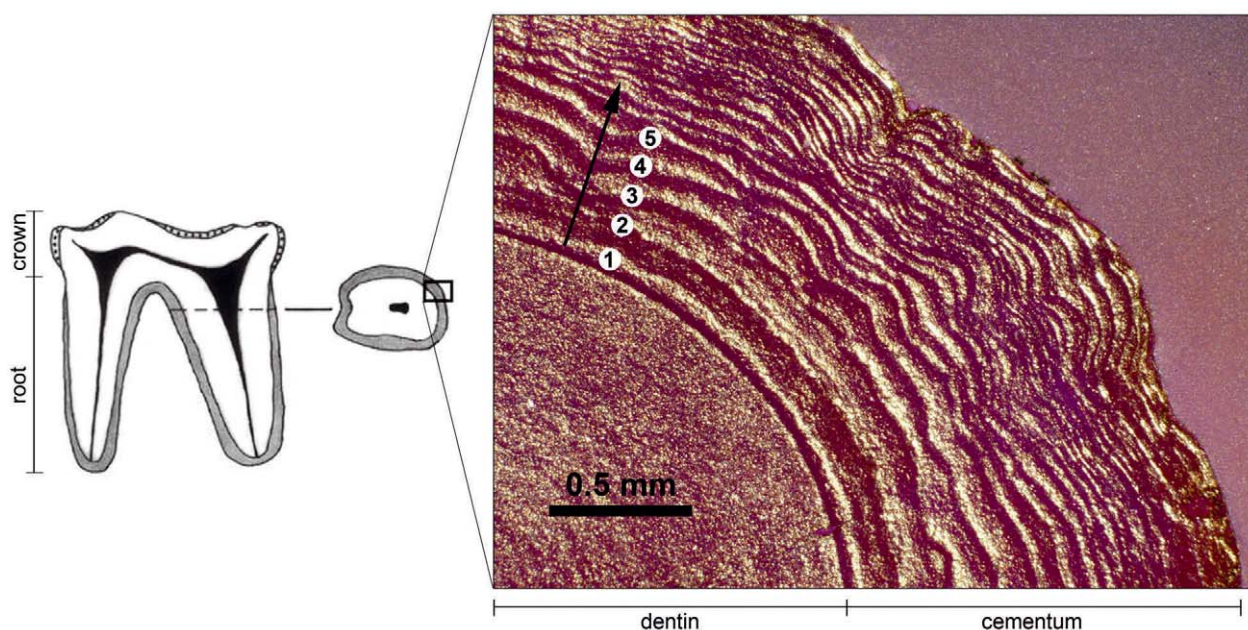


Figure 5: Sketch of M_1 tooth in longitudinal section and cross section through the posterior root in natural size. Pulp cavity: black; dentin: white; cementum: grey. Enlarged detail of etched and coloured cross section of a specimen from Križna jama (KJ 134) is shown on the right. An arrow indicates direction of cementum deposition. The first five cementum annuli are marked with numbers. Individual age estimation: 22–24 years.

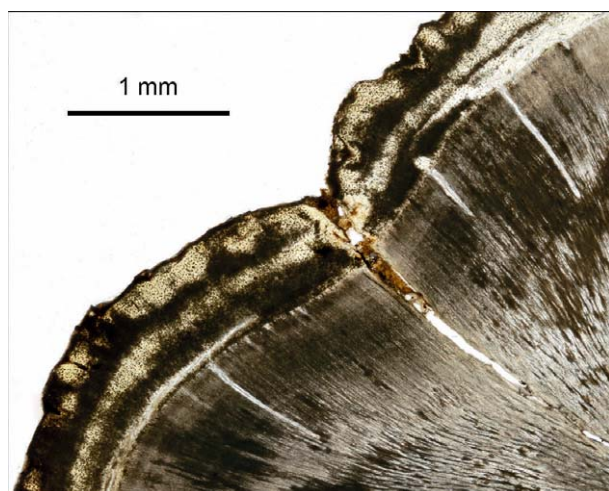


Figure 6: Dental cementum in the thin section of M_1 specimen (KJ 50/1) from Križna jama. Individual age: 3 years. Season at death: early „winter“ (early denning period).

abandon their young at the age of about 2 and a half years; sometimes a year earlier or later (BUNNEL & TAIT, 1981; CRAIGHEAD et al., 1995). Cave bears were probably not different in this respect.

The 9 M_1 specimens from Križna jama belonged to 8–19 year old animals, i.e. prime adults (Table 1). Undoubtedly, these were cave bears at their prime. Modern bears at this age are usually quite fit and have literally no enemies other than man (e.g. McNAMEE, 1997). So why did adult bears die in Križna jama? DIEDRICH (2011a,

b) suggested that two species: Upper Pleistocene hyena (*Crocota crocuta spelaea*) and cave lion (*Panthera leo spelaea*) preyed on hibernating cave bears. There is evidence of both in Križna jama. DIEDRICH pointed out that predation stress of lions and hyenas onto cave bears seems to be one of the main reasons why cave bears hibernated in caves as deep as possible, and were climbing through dangerous and difficult passages in complete darkness to get to the safest place. Also in the case of Križna jama, cave bears hibernated several hundred metres deep inside the cave.

6. Old Bears

Modern brown bears are considered to be *old* after the age of 20 years (CRAIGHEAD et al., 1995). The average life span of brown, polar and black bear is 20–25 years, but under favourable conditions, they can live up to 30 years in the wild (BUNNEL & TAIT, 1981; DEROCHER, 2000). It has long been believed, however, that cave bears could not have lived that long. SOERGEL (1940) was probably the first who assumed that the longevity of the cave bear was considerably reduced, because their teeth wore down more rapidly due to their exclusive herbivore diet, in comparison to omnivorous brown bear. The exposure of pulp cavities led to infections and caused serious dental pathologies that can be frequently observed in cave bear jawbones. Undoubtedly, cave bears could not have gained enough weight before the winter without an efficient feeding apparatus. It can be imagined that this was really a matter of life or death. For this reason, KURTÉN (1958; 1976) expressed doubt that any cave bear lived beyond about

20 years of age. He assumed that the maximum life span was only 15–20 years.

However, analyses of dental cementum in cave bear teeth from Divje babe I and Mokriška jama indicated that cave bears could have lived much longer than previously thought (DEBELJAK, 2007). Accordingly, age determinations of M_1 specimens from Križna jama (Table 1) indicate a moderate increase in the mortality rate not earlier than around the age of 20. In the sample of 26 left M_1 teeth from Križna jama, there are 8 specimens that belonged to cave bears older than 20 years. Mortality in this age group can be attributed to senescence-related malnutrition and vulnerability. M_1 tooth crowns are completely worn only in specimens that belonged to cave bears approximately 25 year old (Table 1; wear stage IX). The oldest age recorded is approximately 28 years, as determined by counting cementum increments in the specimen KJ 118. Interestingly, this is actually the largest M_1 tooth in the sample from Križna jama, which can be quite reliably attributed to a large male. All the evidence indicates that the life span of the cave bear was similar to that of the modern bear species.

7. Age Structure

The age of 28 individual cave bears that died in Križna jama has been determined by the analysis of all left specimens of d_4 milk teeth and M_1 permanent teeth. Only left specimens were taken into consideration to prevent the doubling of data for the same individual. In Figure 7 the frequencies of d_4 and M_1 teeth in different age groups are presented. Figure 8 shows proportions and percentages of juveniles (less than 3 year old animals), subadults (3–4 year old animals), prime adults (5–20 year old animals), and old adults (animals older than 20 years).

The most striking result is the high proportion of old adults (28.6%). The ratio between prime adults and old adults is almost 1:1, the lowest in Slovenian localities that have been studied thus far. More than 30% of all M_1 teeth belonged to animals older than 20 years. For comparison, in the sample of M_1 teeth from Divje babe I, there are only 3.4% of such specimens, from Potočka zijalka 9.6%, and from Mokriška jama 16% (DEBELJAK, 2002; 2004; 2007). Very low proportion of heavily worn teeth has been reported from many other localities, as well (e.g. RABEDER, 1992; GRANDAL D'ANGLADE & VIDAL ROMANÍ, 1997; WEINSTOCK, 1999; 2000; 2001; PACHER, 2000).

Modern bears only die in their denning place on rare occasions (VAN DAELE et al., 1990). If their fat reserves are depleted too early, starving animals leave their den and eventually die somewhere else in case they do not find any food (McNAMEE, 1997). Such behavior could explain the relatively low proportion of old animals in the cave bear localities mentioned above as well. However, Križna jama is a very large cave with long passages, and it seems that it was more common for old, weakened animals to stay in their denning place until their death. One could say that Križna jama was a sort of graveyard for old bears.

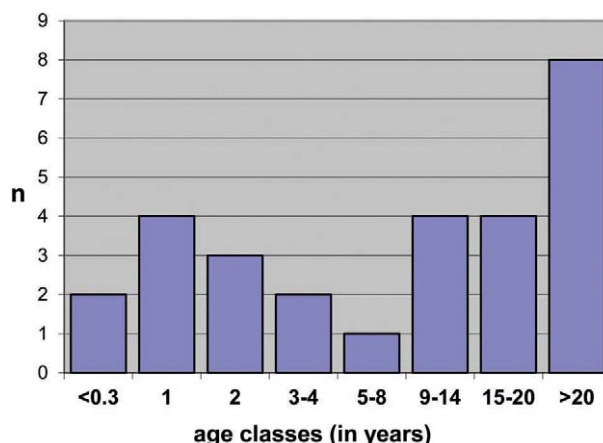


Figure 7: Number of individuals in different age groups (based on 2 left specimens of d_4 and 26 left specimens of M_1).

Another fact has to be taken into consideration when explaining the high proportion of old adults in Križna jama: the number of juveniles is disproportionately low. The number of the youngest, less than 3 month old cubs was expected to be low for the simple reason that milk teeth (d_4) were largely overlooked during the excavations due to their small size. More surprising is the relatively low proportion of yearlings – only about 15%. For comparison: in Divje babe I, Potočka zijalka and Ajdovska jama more than a half of all M_1 specimens belonged to yearlings (DEBELJAK, 2002; 2004; 2011). Only in Mokriška jama, the proportion of yearlings is also relatively low, but still exceeds 20% (DEBELJAK, 2007). The low number of yearlings could partly be explained as the result of male predominance in Križna jama and Mokriška jama. It can be imagined that females with their young avoided caves where adult males would usually hibernate. However, adult males were predominant in Potočka zijalka as well, but the proportion of yearlings was still very high (52.8%). Although juveniles hibernated in Potočka zijalka less frequently than adult males, their mortality rate was much higher, hence their large proportion in the thanatocenosis. Juvenile-dominated age structure has been determined in some other localities where preponderance of males has been established as well (WEINSTOCK, 2000; QUILES & MONCHOT, 2004). Therefore, there must be another reason for the low proportion of yearlings in Križna jama.

The ratio of yearlings to 2-year olds is only 1.33 (4:3) in Križna jama, and 1.42 (27:19) in Mokriška jama. In Potočka zijalka, on the other hand, it is 7.83 (47:6), and in Divje babe (layers 2–10) 6.97 (223:32). There is no logical explanation for such discrepancies between these localities other than taphonomy. As already mentioned in Section 4, the M_1 teeth of yearlings are hollow and have considerably thinner root wall than the same teeth of 2-year-olds. For this reason, teeth of yearlings are much more fragile and prone to destruction. The mortality of yearlings was undoubtedly much higher than the mortality of 2-year-olds.

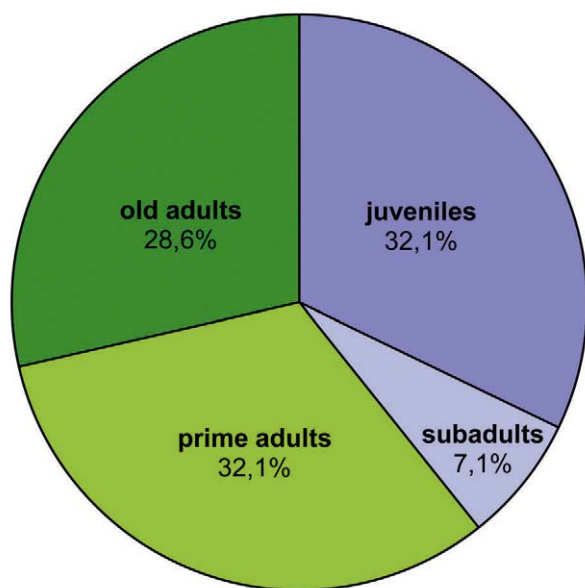


Figure 8: Age structure of the Križna jama cave bear population: pie chart with proportions of different age groups, based on the analysis of d_4 and M_1 teeth.

The ratio of yearlings to 2-year-olds in Potočka zijalka and Divje babe is certainly closer to the actual situation and is a better representation of the original thanatocenosis than the one observed in Mokriška jama and Križna jama. It can be assumed that teeth of yearlings are considerably underrepresented in these two caves due to less favourable taphonomic conditions. This is supported by the fact that the cave bear teeth from Križna jama are generally in a much worse state of preservation than teeth from Divje babe or Potočka zijalka. Dental tissues are heavily corroded. Cave bear remains in Križna jama were often affected by flood water and were all relocated from their original position (RABEDER & WITHALM, 2012).

More fragile skeletal parts (teeth of less than 18 months old individuals) suffered a much higher degree of taphonomic losses during various destructive processes than the mechanically more resistant ones (M_1 teeth of 2-year-olds or older bears). The conditions were more favourable when cave bear remains were buried rapidly in the sediment due to the high sedimentation rate, and remained there relatively undisturbed. This was probably also the case in Potočka zijalka (DEBELJAK, 2004). In my opinion, differences in the proportion of juveniles between various cave bear localities were mainly caused by different taphonomic conditions. The age structure of the original thanatocenosis was undoubtedly influenced by the sex structure of the cave bear population that visited the cave and also by different paleoecological conditions. However, this was later largely blurred by destructive taphonomic processes that affected the remains of various age groups to a different degree.

Data from different cave bear localities can be compared in Figure 9. The proportions of three main age groups in the sample of M_1 teeth are presented in tripolar plot

as proposed by STINER (1994; 1998). Subadults are included in the group of juveniles here. Križna jama, Mokriška jama and Potočka zijalka were populated by a large, highly evolved *Ursus ingressus*, and all three were most frequently used by adult males. However, the age structure of cave bear remains varies considerably between the three localities. Križna jama (red dot) is virtually in the middle of the triangle in Figure 9. This is in no way typical for a cave bear site. The proportion of old adults is larger than normal. The mortality pattern is almost old-dominated. Furthermore, the proportion of juveniles is remarkably low. The age structure of well-preserved cave bear remains from Potočka zijalka (grey dot), on the other hand, is clearly juvenile-dominated. Only the age structure of cave bear remains from Mokriška jama (black dot) corresponds to the classical U-shaped or 'normal non-violent attrition' mortality pattern. Age structure of cave bear remains indicates that the taphonomic conditions in Križna jama were generally the least favourable for the preservation of fossil material of all Slovenian cave bear sites studied so far.

8. Conclusions

Cave bear canines from Križna jama display pronounced sexual size dimorphism which allows clear separation of male and female specimens. Sex structure has been studied on the sample of 67 canines of individuals older than 18 months. More than 73% of them belonged to males. It can be assumed that Križna jama was used as a winter den mostly by adult males.

The predominance of males is particularly notable in the age group of 2–4 year old, still immature bears which indicates that the period of weaning was more critical for males than females. This is in accordance with observations in modern bears.

The age of 28 individual cave bears that died in Križna jama has been determined by the analysis of all left specimens of d_4 milk teeth and M_1 permanent teeth. The presence of two 2–3 month old cubs indicates that females gave birth to cubs in Križna jama during hibernation. The oldest age recorded was reached by a large male that lived for about 28 years. It was determined by counting cementum increments. Another 7 bears from Križna jama lived longer than 20 years. This contradicts the still widespread opinion that cave bears could not reach more than 15–20 years. Data from Križna jama indicate that the life span of the cave bear was not reduced because of its diet. The longevity of the cave bear was basically the same as in modern bears.

The large number of old animals in Križna jama indicates that it was more common for old, weakened animals to stay in their denning place until death than in the majority of other, smaller caves. Possible causes of mortality in juveniles were premature maternal abandonment, malnutrition, injuries, disease, predator attacks and particularly aggression of adult male cave bears. Adult animals could have been killed during the hibernation by cave lions or hyenas.

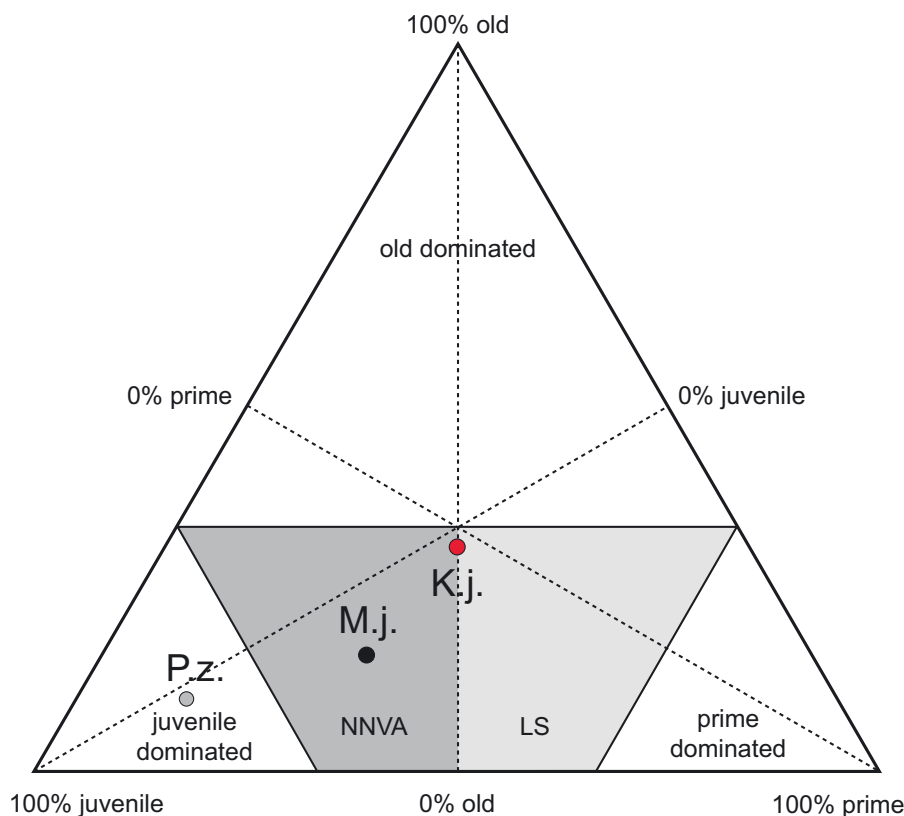


Figure 9: Tripolar plot denoting the proportions of three main age groups in samples of left M_1 teeth from Križna jama (red dot), Mokriška jama (black dot) and Potočka zijalka (grey dot). After STINER (1990; 1994; 1998); dark grey field represents U-shaped or NNVA (normal non-violent attrition) mortality pattern, and light grey LS (living structure) pattern.

Season at the time of death has been estimated for 10 younger individuals by the analysis of tooth development and by examining the last cementum increment when possible. The majority of deaths occurred in the winter, during denning. It is possible, however, that some bears died in the cave before or shortly after the hibernation period as well.

The age structure of cave bear remains from Križna jama is not typical for a cave bear site. The proportion of old bears is unusually large (28.6%), while the proportion of juveniles is remarkably low (32.1%). Only about 15% of all M_1 teeth belonged to yearlings, in comparison to some other Slovenian sites where specimens of this age group absolutely prevail with more than a 50% share. This could be partly explained as the result of male predominance in Križna jama.

Furthermore, it can be assumed that differences in the proportion of juveniles between various cave bear localities were mainly caused by different taphonomic conditions. The age structure of the original thanatocenosis was undoubtedly influenced by the sex structure of the cave bear population that visited the cave and also by different paleoecological conditions. However, this was later largely blurred by destructive taphonomic processes that affected the remains of various age groups to a different degree. Very low proportion of hollow, fragile teeth of animals younger than 18 months reflects unfavourable preservational conditions in Križna jama. Cave bear remains were badly affected by flood water. Its effect can also be observed in severely damaged dental tissues.

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