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Estimating the extinction time of two cave bears, *Ursus spelaeus* and *U. ingressus*

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Abstract. Although cave bear remains have been described since the end of 18th century, recent discoveries and methods provide new knowledge about the typical representative of Pleistocene megafauna, which did not survive the Last Glacial Maximum. Genetic studies supplemented by morphometric analyses showed that this mammal differentiated in the Late Pleistocene into two main forms called *Ursus spelaeus* and *U. ingressus*. The latter is regarded more expansive and replaced the native *U. spelaeus* in some areas of Western Europe. Taking into account the differences between these bears, it is interesting to determine if these forms became extinct at different or similar times. Therefore, we assessed their extinction times, applying seven methods using 205 dated records of cave bear ascribed to these two forms. The average extinction time of *U. spelaeus* was about 25,600 cal. yr BP (Before Present) and of *U. ingressus* about 24,800 cal. yr BP. The estimations showed that that *U. ingressus* could survive up to ca. 1,000 years longer than its relative *U. spelaeus*. The longer survival of the former could be related to its greater morphological variability and better adaptation to arid continental environments, as well as a stronger tendency to occasional omnivory. Both bears became extinct within the coldest phase of the last glacial period, Greenland Stadial 3, which implies that climate cooling was the main factor of their extinction. The climate deterioration decreased vegetation productivity, and could also have had negative consequences on the prolonged hibernation period when the bears were more susceptible to the activity of humans and predators.

Key words: ^{14}C dating, cave bear, extinction, Last Glacial Maximum, megafauna, Pleistocene, radiocarbon dates, *Ursus spelaeus*, *Ursus ingressus*.

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I. INTRODUCTION

The cave bear (*Ursus spelaeus sensu lato*) is the typical representative of the Pleistocene megafauna, which went extinct before the Last Glacial Maximum (LGM) (PACHER and STUART 2009; BACA et al. 2017). It emerged gradually from the Middle Pleistocene *Ursus deningeri* before the Last Interglacial (MAZZA and RUSTIONI 1994; RABEDER et al. 2000) and then spread across Eurasia during the Late Pleistocene. For an extended period of time, the Late Pleistocene remains of cave bears were described under one species name *Ursus spelaeus*, but the study of ancient DNA extracted from its fossils (RABEDER and HOFREITER 2004; RABEDER et al. 2004a; RABEDER et al. 2004b; KNAPP et al. 2009; BACA et al. 2012; BACA et al. 2014; STILLER et al. 2014), and detailed morphometric analyses of metapodial bones, skulls and teeth (MÜNZEL and ATHEN 2009; BARYSHNIKOV and PUZACHENKO 2011; BACA et al. 2012) showed that at least two distinct forms, or perhaps species of the cave bear, existed. The genetic study allowed recognition of two main haplogroups: *Ursus spelaeus* sensu stricto and *U. ingressus* (RABEDER et al. 2004a), which most likely diverged between 414,000 and 173,000 years ago (KNAPP et al. 2009), and occupied different geographic regions. *U. spelaeus* inhabited mainly Western Europe but migrated also to the Altai (KNAPP et al. 2009), whereas *U. ingressus* lived in south-eastern and Central Europe as well as in the Ural region.

U. kudarensis is considered the third species (STILLER et al. 2014), which is known from the Caucasus and the Yana River region in eastern Siberia (BARYSHNIKOV 1998; KNAPP et al. 2009). This species evolved before the separation of *U. spelaeus* and *U. ingressus* (KNAPP et al. 2009; DABNEY et al. 2013; STILLER et al. 2014; BACA et al. 2016). Within *U. spelaeus*, besides being the typical large bear (*U. spelaeus spelaeus),* two dwarf forms were described: *U. spelaeus eremus* and *U. spelaeus ladinicus* from the high alpine caves in Austria and Italy (RABEDER and HOFREITER 2004; RABEDER et al. 2004a; RABEDER et al. 2008). Another small cave bear, *U. rossicus*, which occupied the territory from the Ukraine to Transbaikalia (BARYSHNIKOV and FORONOVA 2001), appeared genetically closely related to *U. ingressus* (STILLER et al. 2014; BACA et al. 2016).

U. ingressus has been regarded as a species ecologically better adapted to continental environments, and could effectively compete with *U. spelaeus* (BARYSHNIKOV and PUZACHENKO 2011). In accordance with that, *U. ingressus* migrated into the Alps from the east around 50,000 years ago and replaced the native populations of *U. s. eremus* and *U. s. ladinicus* (RABEDER and HOFREITER 2004; RABEDER et al. 2008). A similar replacement happened about 32,500 years ago in the Ach valley in south-western Germany, where *U. ingressus* displaced the typical *U. s. spelaeus* (HOFREITER et al. 2007; MÜNZEL et al. 2011). However, in the Totes Gebirge in Austria, these two species coexisted for a long time in closely located sites without hybridisation and interactions (HOFREITER et al. 2004a).

The recent estimation of the cave bear extinction, including the latest cave bear remains from Stajnia Cave in Poland which dated to 20,930 ± 140 ^{14}C yr BP, indicates that this mammal vanished 26,100-24,300 cal. yr BP within the coldest phase of the last glacial period, Greenland Stadial 3 (GS-3) before the LGM, similarly to other megafauna representatives. However, these calculations were carried out on cave bear records without their distinction between the main groups: *U. spelaeus* and *U. ingressus*. Taking into account the difference between these two forms and more expansive character of the latter, it seems interesting to assess if these two cave bears became extinct at different or similar times. Therefore, we conducted new estimations of extinction time separately for these species, including newly published dates. Our new calculations showed that *U. ingressus* could survive up to ca. 1,000 years longer than its relative *U. spelaeus*.

II. MATERIALS AND METHODS

The estimation of the extinction time was based on the dates of cave bear remains collected in previous analyses (PACHER and STUART 2009; BACA et al. 2016), which we enriched with dated records obtained by other authors including recent findings (CECH et al. 1997; DAVIES and HEDGES 2008-2009; DÖPPES et al. 2011; DÖPPES et al. 2016; FORTES et al. 2016). In the study, we included the latest dates reported for *U. ingressus* phalanx discovered in Stajnia Cave in Poland. The specimen was found during excavations, which have been started since 2006, and were conducted under the direction of Paweł SOCHA, responsible for paleontological works, and Mikołaj URBANOWSKI, responsible for archaeological works. They made a significant contribution to the discovery of this specimen. The cave material was deposited over 100,000 years, and differentiated into six stratigraphical complexes (ŻARSKI et al. 2017). The cave bear phalanx was found at the bottom of the layer C18 deposited during the Leszno (Brandenburg) Phase.

All dates were carefully selected. We used only radiocarbon ^{14}C dates and discarded those based on molecular, uranium series, uranium/thorium, stratigraphy context and strata dating. Moreover, we did not include dates without dating error, infinitive dates and dates out of range 47,500 ± 3,000 BP after calibration. In the case of repeated dates obtained from the same specimen found in Schreiberwandhöhle and Stajnia Cave, we averaged the calibrated outcome. Finally, we gathered 119 dates ascribed to *U. spelaeus* and 86 to *U. ingressus* species. The attribution of the dates to the cave bear forms was supported by genetic studies and the geographic distribution of samples. Dates of remains with unclear affiliation were excluded. The dates were calibrated to the (BP) in OxCal v4.2.4 (BRONK RAMSEY et al. 2013) using intCal13 atmospheric curve (REIMER et al. 2013). The received calibrated mean values and standard deviations were used in the estimation of the extinction time.

The extinction time was estimated using five methods proposed by STRAUSS and SADLER (1989), SOLOW (1993), ROBERTS and SOLOW (2003), SOLOW and ROBERTS (2003) and MCINERNY et al. (2006), and implemented by RIVADENEIRA et al. (2009). Moreover, we applied the inverse-weighted Gaussian-resampled (GRIWM) (BRADSHAW et al. 2012) and bootstrap-resampled (BRIWM) methods (SALTRÉ et al. 2015) assuming 10,000 iterations and α level 0.05. The Wilcoxon signed-rank test and log likelihood ratio (G-test) test of independence with the Williams' continuity correction were conducted in R package (R_CORE_TEAM 2015).

III. RESULTS

The excavation sites in which dated remains of two cave bears were found widely cover the whole range of cave bear distribution in Europe (Fig. 1). The dated fossils of *U. spelaeus* were excavated in 35 sites, whereas those of *U. ingressus* in 32. In three caves, the two forms were found. The dates later than 30,000 cal. yr BP represent various regions in Europe: Iberian Peninsula, Alps with adjacent regions, Italian Peninsula, Carpathian Mountains and the Kraków-Częstochowa Upland in Poland (Fig. 1, Fig. 2).

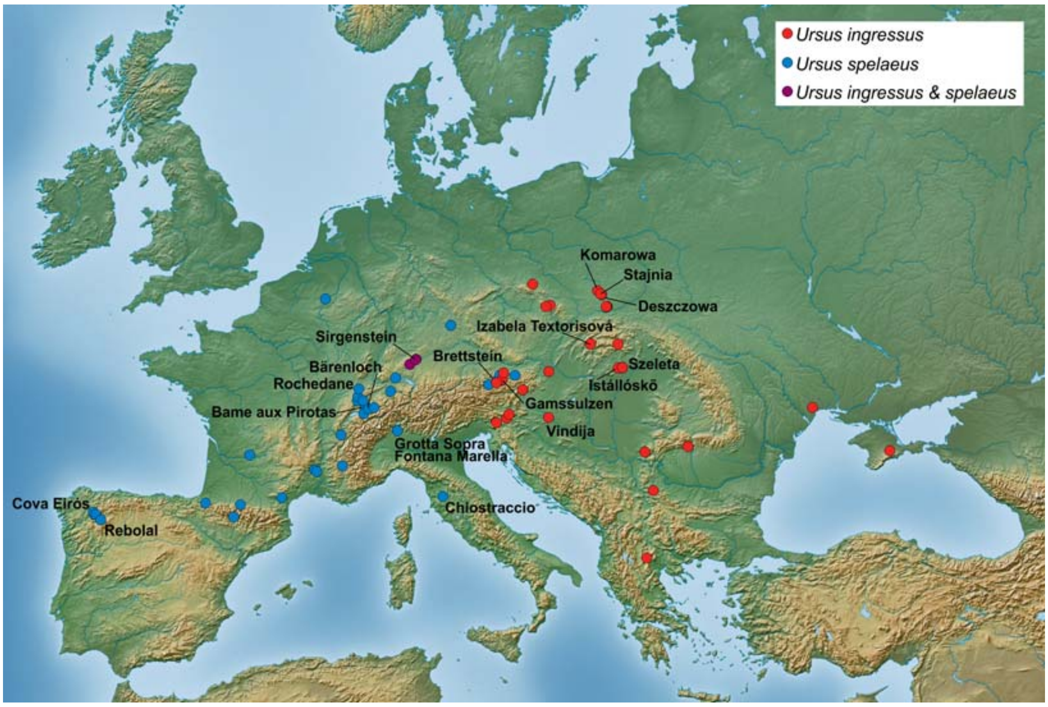

Fig. 1. Localization of sites with dated cave bear records which were used in the study. The sites with samples later than 30,000 cal yr. BP were marked by their names. The sites were coloured according to the form of cave bear found in the given site.

So far the latest date was reported for *U. ingressus* phalanx found in Stajnia Cave in Poland (BACA et al. 2016). The specimen was confirmed genetically and dated independently in two laboratories, which provided the ^{14}C date 20,930 ± 140 yr BP (25,251 cal. yr BP) and 21,900 ± 90 yr BP (26,114 cal. yr BP). In the calculations, we used the average value 25,682.5 ± 159 cal. yr BP. The dating is in good agreement with the stratigraphic context of the layer in which the specimen was found (ŻARSKI et al. 2017). The layer was accumulated during the Leszno (Brandenburg) Phase dated to 20.1-23.7 (±1.1 to 2.4) ka (MARKS 2012; MARKS et al. 2015).

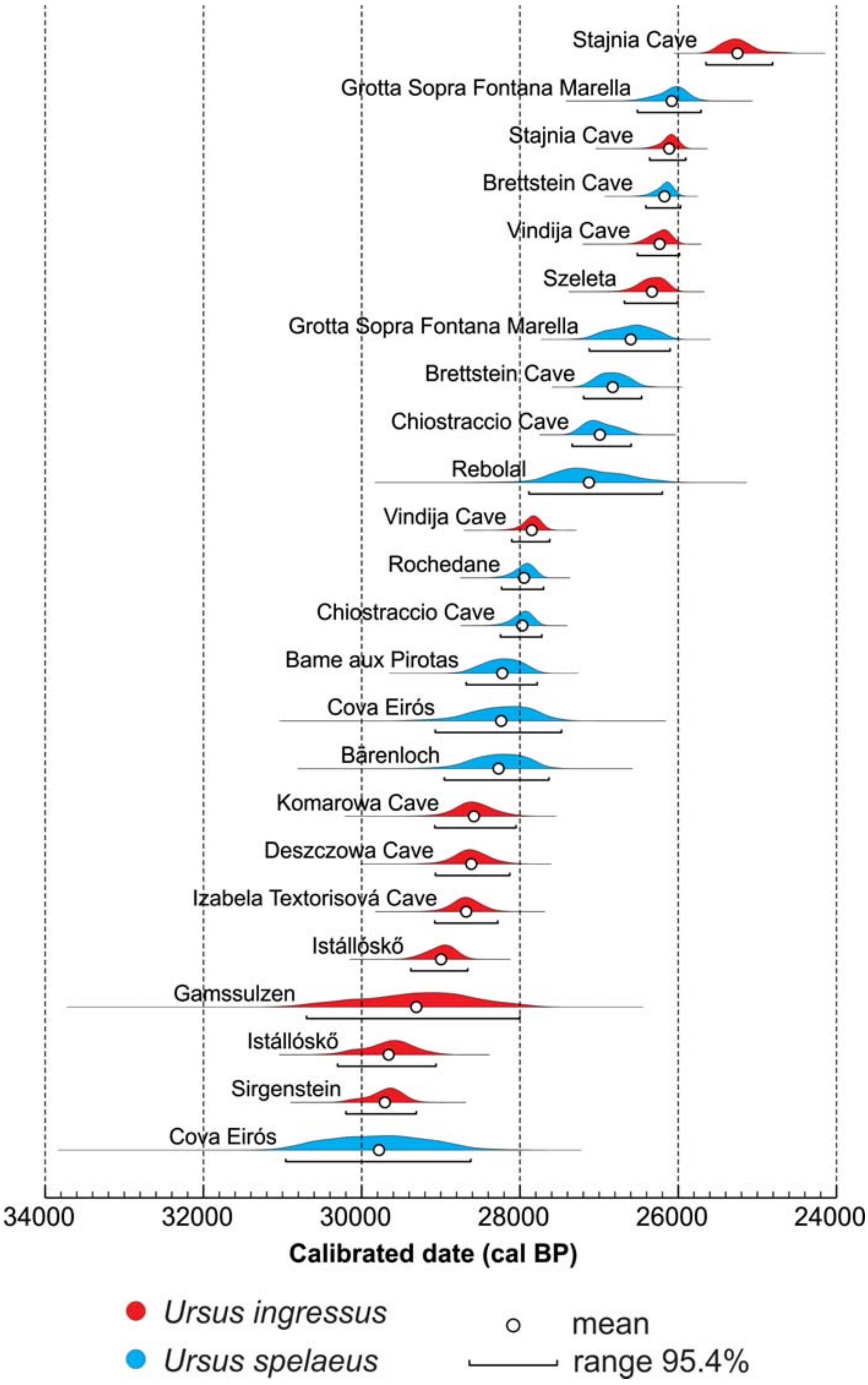

Fig. 2. Likelihood distributions of calibrated dates for cave bear samples later than 30,000 cal yr. BP. The plots were coloured according to the form of cave bear. Plots for two independent datings of the sample from Stajnia Cave are shown separately.

The next late date with the age 21,810 ± 200 yr BP (26,082 ± 202 cal. yr BP) was received for remains found in Grotta Sopra Fontana Marella in Italy, represented most likely by *U. spelaeus* (PEREGO et al. 2001). Slightly older are fossils found in Brettstein Cave in Austria: 21,970 ± 70 yr BP (26,174 ± 111 cal. yr BP) ascribed to *U. spelaeus eremus* or *U. spelaeus ladinicus* (DÖPPES et al. 2016). The next late samples affiliated to *U. ingressus* come from Vindija Cave in Croatia (HOFREITER et al. 2004b): 22,020 ± 100 yr BP (26,235 ± 137 cal. yr BP) and Szeleta Cave in Hungary (ADAMS 2002): 22,107 ± 130 yr BP (26,331 ± 175 cal. yr BP). Some caves were occupied by the bears for a longer period because their older remains were also found in them, e.g. in Grotta Sopra Fontana Marella (since at least 26,600 cal. yr BP), in Brettstein Cave (since at least 39,330 cal. yr BP), in Vindija Cave (since at least 46,184 cal. yr BP), and in Szeleta Cave (since at least 46,450 cal. yr BP). Stajnia Cave was also inhabited continuously for a long time because numerous remains of the cave bear were found across the whole profile from layers dated to more than 100,000 years (ŻARSKI et al. 2017).

The collected dates enabled the estimation of extinction time of two cave bears using seven methods (Table 1). All estimations for *U. ingressus* were smaller in comparison to those for *U. spelaeus.* Five of the methods used by STRAUSS and SADLER (1989), SOLOW (1993), MCINERNY et al. (2006), SALTRÉ et al. (2015) and BRADSHAW et al. (2012), provided highly consistent estimations for the individual bears. The average extinction time of *U. spelaeus* was 25,573 cal. yr BP, and the range between the maximum and minimum was only 52 years. The average time for *U. ingressus* was smaller, i.e. 24,826 cal. yr BP with the range 270 years. The difference between the estimations depending on methods ranged from 700 to 915 years (747 on average). The extinction time of *U. ingressus* was significantly later than that of *U. spelaeus* (Wilcoxon test, p-value = 0.031).

Only the methods by ROBERTS and SOLOW (2003) and SOLOW and ROBERTS (2003) gave deviated estimations. The extinction time of *U. spelaeus* calculated by these methods was more than 1,100 years later in comparison to the other five methods. The time of *U. ingressus* extinction was also consequently much later, i.e. 21,025 or even 15,185 cal. yr BP,

Table 1

Estimated extinction times (cal. yr BP) of two cave bears using seven methods. For the first five methods the upper boundary of 95% confidence interval is presented. For BRIWM and GRIWM methods, median and 95% confidence interval (in parentheses) are shown

Method	*Ursus spelaeus*	*Ursus ingressus*	Difference
GRIWM (BRADSHAW et al. 2012)	25,590 (25,035-26,096)	24,866 (24,426-25,471)	724
BRIWM (SALTRÉ et al. 2015)	25,538 (25,030-26,210)	24,623 (24,104-27,015)	915
(STRAUSS & SADLER 1989)	25,573	24,868	705
(SOLOW 1993)	25,578	24,878	700
(MCINERNY et al. 2006)	25,586	24,893	693
(ROBERTS & SOLOW 2003)	24,422	21,025	3,397
(SOLOW & ROBERTS 2003)	24,334	15,185	9,149

respectively. Considering all the seven methods, *U. ingressus* became extinct also significantly later than *U. spelaeus* (Wilcoxon test, p-value = 0.008). However, the methods by ROBERTS and SOLOW (2003) and SOLOW and ROBERTS (2003) are prone to the type II errors and are regarded the most conservative. They can give very broad confidence limits with the range greater than the nominal value. Their calculations can even show that an already extinct species is still living (RIVADENEIRA et al. 2009). Therefore, the results of these methods should be considered with caution.

The most solid is regarded the GRIWM method because it provides model accuracy and no misclassification issues. This approach uses inherent down-weighting interval procedure and takes into account the uncertainties in dating samples (SALTRÉ et al. 2015). The 95% confidence interval of extinction time calculated by this method contains the estimated times of the other four consistent methods for the individual bears (Table 1). Comparing the extreme limits of these intervals, the maximum difference between the extinction times of the two cave bears could be 1,670 years.

In Fig. 3, we compared the estimated extinction times with the distribution of the cave bear records, and the revised Greenland ice core $\delta^{18}O$ curve obtained by combining the

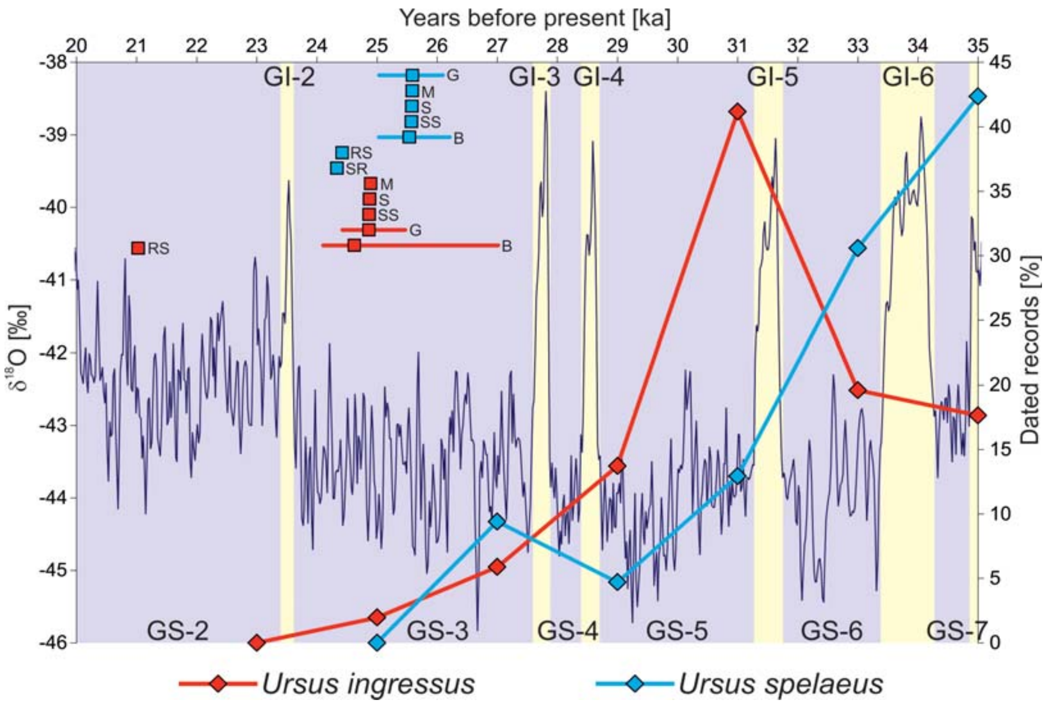

Fig. 3. Distributions of late dates of the cave bear samples later than 35,000 ka (red and blue lines with diamonds). The diamonds mean the percent of remains dated to the given age ± 1000 years. Rectangles indicate extinction times for two cave bear forms, estimated by methods: STRAUSS and SADLER (1989) (SS), SOLOW (1993) (S), MCINERNY et al. (2006) (M), SOLOW and ROBERTS (2003) (SR), ROBERTS and SOLOW (2003) (RS), BRIWM by SALTRÉ et al. (2015) (B) and GRIWM by BRADSHAW et al. (2012) (G). Horizontal bars indicate 95% confidence interval for the BRIWM and GRIWM methods. The results were compared with the revised Greenland ice core $\delta^{18}O$ curve (in dark blue) developed by combining the Cariaco Basin (Hulu Cave) and Greenland ice core (GICC05) records (COOPER et al. 2015). Corresponding Greenland stadials (GS) and interstadials (GI) were marked.

Cariaco Basin (Hulu Cave) and Greenland ice core (GICC05) records (COOPER et al. 2015). The curve is a good climate proxy and reflects climatic changes during the Pleistocene. Most of the estimated extinction times of the two cave bears fall within the Greenland Stadial 3 (GS-3). The five consistent estimations for *U. spelaeus* are placed in the middle of this stadial, whereas those for *U. ingressus* are shifted to its second half. The extinction time calculated by ROBERTS and SOLOW (2003) method corresponds to the GS-2 Stadial.

The distribution of *U. spelaeus* dated records starts to decline since about 35,000, whereas such records for *U. ingressus* begin to decrease steadily about 4,000 years later (Fig. 3). The difference between these two distributions is statistically significant (G-test, p-value = 0.0008). Assuming that the analysed records are representative and correspond to the size of the cave bear population, we can conclude that the extinction of *U. spelaeus* started earlier than *U. ingressus*.

IV. DISCUSSION

Our calculations of extinction time of the two main cave bear lineages, *U. spelaeus* and *U. ingressus*, imply that they did not survive into the Last Glacial Maximum (LGM), if we accept the strict definition of its duration from 23,000 to 19,000 cal. yr BP (WAELBROECK et al. 2009). However, assuming the earlier beginning of this period, i.e. since 26,000 (PELTIER and FAIRBANKS 2006) or 26,500 cal. yr BP (CLARK et al. 2009), these mammals became extinct at the beginning of the LGM. Nevertheless, the calculated extinction times of the cave bears coincide with the end of the first megafaunal transition, which started in Greenland interstadials 5 to 7, and finished at the beginning of the LGM in northern Europe (COOPER et al. 2015). Therefore, the cave bear extinction represents the pre-LGM megafaunal disappearance. The second megafaunal transition occurred after the LGM, at the end of the stadial GS-2 and finished at the beginning of the Holocene (COOPER et al. 2015).

Although, the decline of cave bear populations may have started even 50,000 years ago (STILLER et al. 2010), the estimated extinction times indicate that two cave bear species vanished within the GS-3 stadial, which is one of the coldest and the longest in the last glacial period. According to the Greenland ice core $\delta^{18}O$ curve, this period lasted about 4,000 years. Therefore, it is reasonable to assume that the climate cooling could be the main factor of cave bear extinction (STUART and LISTER 2007; PACHER and STUART 2009; BACA et al. 2016), especially if we take into account that this mammal was a strict herbivore, as it is supported by the morphology of skull and dentition (KURTÉN 1976; MATTSON 1998; RABEDER et al. 2000; GRANDAL-D'ANGLADE and LOPEZ-GONZALEZ 2004; VAN HETEREN et al. 2009; VAN HETEREN et al. 2014), enamel thickness and structure (MACKIEWICZ et al. 2010; WISZNIOWSKA et al. 2010) and numerous studies of stable isotopes ($\delta^{13}C$, $\delta^{15}N$) of its remains (BOCHERENS et al. 1994; BOCHERENS et al. 1997; NELSON et al. 1998; VILA TABOADA et al. 1999; FERNÁNDEZ-MOSQUERA et al. 2001; BOCHERENS et al. 2006; BLANT et al. 2010; HORACEK et al. 2012; PACHER et al. 2012; KRAJCARZ et al. 2014; KRAJCARZ et al. 2016). As a consequence of the climate deterioration, the quality and availability of plant food, being the crucial component of cave bear diet, decreased.

The temperature drop could also prolong the hibernation period of the cave bears (RABEDER et al. 2000), during which this animal was more prone to hunting by humans (KURTÉN 1958; GRAYSON and DELPECH 2003; STILLER et al. 2010; BON et al. 2011; MÜNZEL et al. 2011; WOJTAL et al. 2015) and attacks by large carnivores (BOCHERENS et al. 2011a; DIEDRICH 2014). The importance of caves for these bears as hibernation sites, for which they had to compete with humans and other carnivores, could be another reason of their extinction (GRAYSON and DELPECH 2003). The recent study of genetic diversity of cave bears in Spain revealed that individual caves were almost exclusively inhabited by unique haplotype lineages, which implies that the cave bears, in contrast to the brown bear, returned to the cave where they were born and formed stable maternal social groups for hibernation (FORTES et al. 2016). The fidelity to the birth site could decrease the probability of finding a proper hibernation site, when the original cave was already occupied by humans, cave lion (*Panthera spelaea*) or cave hyena (*Crocuta crocuta spelaea*).

In light of the proposed reasons of the cave bear extinction, it is interesting to hypothesise why *U. ingressus* could survive longer than *U. spelaeus*, as it is indicated by our calculations. BARYSHNIKOV and PUZACHENKO (2011) assumed that *U. ingressus* was ecologically better adapted to continental environments than *U. spelaeus*, and could win the competition for food and hibernation site, especially during a cold and arid climate. In agreement with that, there are known examples that *U. ingressus* expanded and replaced *U. spelaeus* leading to its extinction (RABEDER and HOFREITER 2004; HOFREITER et al. 2007; RABEDER et al. 2008; MÜNZEL et al. 2011). The better adaptational abilities of *U. ingressus* can be associated with its greater morphological variability in comparison to *U. spelaeus* (RABEDER et al. 2008). *U. ingressus* showed more advanced morphodynamic indices of teeth, which suggest an improved masticatory performance (RABEDER et al. 2008). It could allow for more efficient food processing and quicker accumulation of fat especially before the hibernation period.

The longer survival of *U. ingressus* could be also related with the larger flexibility in dietary habit, e.g. a tendency to omnivory. Actually, remains found at south-eastern European sites (Romania), likely belonging to *U. ingressus*, showed larger values of $\delta^{15}N$ isotope, which imply that this cave bear could enrich its diet with animal proteins (RICHARDS et al. 2008; ROBU et al. 2013). The omnivorous diet was also suggested for *U. ingressus* samples found in Loutra Arideas Cave in Greece, which showed the wider and larger values of $\delta^{13}C$ isotope (DOTSIKA et al. 2011). This bear probably supplemented its diet with terrestrial and more likely aquatic animal proteins. Other studies showed that *U. spelaeus eremus* and *U. ingressus* living in closely located caves in Austria were characterised by the disparate isotopic composition (BOCHERENS et al. 2011b; MÜNZEL et al. 2014). It was interpreted that the bears consumed different plant types in various habitats.

However, the omnivory of cave bears deduced from the isotopic analyses was criticised (BOCHERENS et al. 2014b). The additional analyses showed that the isotopic characteristic of Romanian cave bears overlap with that of the most herbivorous modern brown bears and clearly differ from more carnivorous modern brown bears. Moreover, these Romanian cave bears are similar in this respect to two Pleistocene herbivores: the woolly mammoths and the fallow deer (BOCHERENS 2015). The recent more comprehensive study did not confirm the taxonomic and geographic differentiation of the isotopic composition of cave bear samples (KRAJCARZ et al. 2016). The samples found in high Alpine sites and two Romanian caves, Peţtera cu Oase and Urţilor, were exceptions but they were not regarded as evidence for the omnivory of cave bears. It is not easy to interpret the isotopic data because the results are under the influence of many other factors unrelated to diet, such as individual age, environmental conditions, climate, physiology and hibernation length (PACHER and STUART 2009; GRANDAL-D'ANGLADE et al. 2011). Nevertheless, even if the cave bears appear homogeneous in the global scale in respect to their diet, it cannot be excluded that *U. ingressus* could be occasionally more flexible than *U. spelaeus* in its dietary habits, which enabled its longer survival.

The distribution of the latest records of cave bear is not restricted to some special geographic areas. It implies that this mammal was vanishing simultaneously in various regions of its whole former range in Europe and not from the east to west direction as it was previously assumed (STILLER et al. 2014). However, the cave bear could locally find refugial habitats with sufficient plant productivity, in which it could survive longer (BACA et al. 2016). One of such places could be karst regions offering a suitable microclimate beneficial for plants and animals. Such regions could be for example the Montagnola Senese with Chiostraccio Cave in Italy and the Kraków-Częstochowa Upland with Stajnia Cave in Poland (MARTINI et al. 2014; BACA et al. 2016).

The estimation of the extinction time is influenced by the quality of dating records. It cannot be excluded that later specimens will be discovered in the future and the extinction time will turn out later. However, the late dates should be considered with caution because samples that were carbonated or contaminated by more recent carbon can show rejuvenated dates. The similar problem concerns samples with poorly-preserved collagen. There are several post-LGM remains of cave bear with dates below 18,000 yr BP that should be verified (KOSINTSEV et al. 2003; GRANDAL D'ANGLADE et al. 2006). In fact, some late dates of cave bears after the second dating turned out to be much older (MÜNZEL and ATHEN 2009; BLANT et al. 2010; BOCHERENS et al. 2014a).

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