Historical Biology
An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

Extinction pattern of Alpine cave bears - new data and climatological interpretation

Doris Döppes, Gernot Rabeder, Christine Frischauf, Nadja Kavcik-Graumann, Bernd Kromer, Susanne Lindauer, Ronny Friedrich & Wilfried Rosendahl

To cite this article: Doris Döppes, Gernot Rabeder, Christine Frischauf, Nadja Kavcik-Graumann, Bernd Kromer, Susanne Lindauer, Ronny Friedrich & Wilfried Rosendahl (2019) Extinction pattern of Alpine cave bears - new data and climatological interpretation, Historical Biology, 31:4, 422-428, DOI: 10.1080/08912963.2018.1487422

To link to this article: https://doi.org/10.1080/08912963.2018.1487422

Published online: 18 Jun 2018.

HISTORICAL BIOLOGY
2019, VOL. 31, NO. 4, 422–428
https://doi.org/10.1080/08912963.2018.1487422

Taylor & Francis
Taylor & Francis Group

ARTICLE

Extinction pattern of Alpine cave bears - new data and climatological interpretation

Doris Döppes[a], Gernot Rabeder[b], Christine Frischauf[b], Nadja Kavcik-Graumann[c], Bernd Kromer[d], Susanne Lindauer[d], Ronny Friedrich[d] and Wilfried Rosendahl[a,d]

[a]Reiss-Engelhorn-Museen, Mannheim, Germany; [b]Institute of Palaeontology, University Vienna, Vienna, Austria; [c]Department of Cognitive Biology, University Vienna, Vienna, Austria; [d]Curt-Engelhorn-Center Archaeometry gGmbH, Mannheim, Germany

ABSTRACT
Cave bears have disappeared from the Alps from different altitudes at different times. The temporal progression of the HDEL (Height Dependent Extinction Line) – a compilation of the geologically most recent radiocarbon dates per altitude level – is not consistent with the general cooling of the temperatures from about 45 ka BP. The cave bear sites of the Northern Alps with the most recent radiocarbon ages are not situated in the lowlands but in caves in altitudes of 1,500 m to 1,700 m above sea level (a.s.l.).

Cave bears fed almost exclusively on herbs and leaves. It was assumed that with the general cooling in the OIS 3 since about 45 ka BP also the migration of the alpine elements into the lowlands took place. It could be recognized that the populations in the lower situated cave bear site became earlier extinct than the cave bear population in the higher altitudes.

With new radiocarbon dates, done at the Curt-Engelhorn-Center Archaeometry at the Reiss-Engelhorn-Museen in Mannheim (Germany), the HDEL can be determined much more precisely and the causes of gradual extinction are also better understood.

ARTICLE HISTORY
Received 27 April 2018
Accepted 7 June 2018

KEYWORDS
Cave bears; radiocarbon dating; Alps; extinction pattern

Introduction

The cave bear was one of the most impressive animals of the Late Pleistocene in Europe and western Asia and is divided into two major mitochondrial clades, *U. ingressus* and *U. spelaeus* (*U.s. ladinicus, U.s. eremus, U.s. spelaeus*, Stiller et al. 2014). Cave bears were strict herbivores (e.g. Bocherens 2015) and used amongst others caves for hibernation. In contrast studies of some cave bears suggested a substandial amount of meat (e.g. Figueirido et al. 2009; Robu et al. 2013; Jones and DeSantis 2016). Cave bears became extinct in the Alps around 26 ka calBP (Döppes et al. 2016).

In order to determine the HDEL (Height Dependent Extinction Line) the youngest radiocarbon dates from cave bears per alpine altitude levels are combined. The course of the HDEL is in contrast to the previous assumption that the extinction of the alpine cave bears would have been caused by the temperature decline 40,000 years ago. According to this previous model (Rabeder et al. 2017b), the HDEL would have to gradually decrease from about 45,000 cal BP at 2,800 m a.s.l. to 26,000 cal BP at 190 m a.s.l. and assume the most recent geological cave bear date for the lowest located caves.

Recent data does not support this conclusion: the HDEL runs from the highest cave bear deposits on 2,800 m a.s.l. (Conturines cave) on 2,250 m a.s.l. (Schreiberwand cave) to the caves around 2,000 m a.s.l. (e.g. Ramesch-Bone Cave, Hille and Rabeder 1986) and to the caves between 1,550 m to 1,700 m a.s.l. (Brettstein bear cave, Schlenken Passage cave), which provided the youngest ages. The main purpose of the article is to explain the peculiar course of the HDEL. Why did the HDEL extend – in view of the approaching cold phase of the Würmian High glacial – not synchron with the decrease of the geological time and the reduction of the altitude? A climatological explanation is attempted.

Methods and material

Method

Radiocarbon dating was done on 28 cave bear bones from nine sites at the Curt-Engelhorn-Centre Archaeometry (CEZA) employing standard sample pre-treatment methods for bone samples, combustion of the samples using an Elemental Analyzer and radiocarbon-determination using a MICADAS AMS (Accelerator Mass Spectrometry) system (see Döppes et al. 2016). Samples with lab codes including 'MAMS' as an identifier are analyzed in that lab and are calibrated by SwissCal1.0 (L. Wacker, ETH-Zürich) using the calibration dataset IntCal13 (Table 1, Figure 1).

The fossil material comes exclusively from bones of alpine cave bear (Table 1), recovered during excavations, excursions and sample collections by members of the Institute of Palaeontology, University Vienna. All bone samples were taxonomically determined by comparing them with the extensive material of cave bears of the Institute for Paleontology of the University of Vienna. Particular care was taken to ensure that the remains are from cave bears and excludes the belonging to the brown bear.

CONTACT Doris Döppes doris.doeppes@mannheim.de Reiss-Engelhorn-Museen, Mannheim, Germany

Published online 18 Jun 2018

Table 1. AMS dating from Alpine cave bear bones by the Curt-Engelhorn-Centre Archaeometry (CEZA).

MAMS-no.	cave name	state	altitude (m)	taxon	sample (bone)	C/N	delta C13 AMS	collagen (%)	C14_age (years BP)	error 1-sigma	calibrated age SwissCal (calBP)	references
14,895	Conturines	I	2800	*U. ladinicus*	mt 3/4	3.1	−25.6	8.6	40,190	950	44,840–43,370	new
14,896	Conturines	I	2800	*U. ladinicus*	mt 4	3.2	−22.0	13.6	>49,000			new
14,909	Schreiberwand	A	2250	*U. s. eremus*	ph 1 fragment	3.2	−23.1	9.0	43,000	480	46,430–45,590	new
14,910	Schreiberwand	A	2250	*U. s. eremus*	ph 1 fragment	3.2	−22.2	9.8	45,770	650	48,051–46,618	new
18,215	Bärenfalle	A	2100	*U. s. eremus*	mand fragment	3.2	−22.2	5.3	48,740	800	>49,000	new
14,893	Brettstein	A	1660	*U. s. eremus*		3.1	−20.5	7.7	22,510	120	27,580–26,940	Döppes et al. 2016
17,800	Brettstein	A	1660	*U. s. eremus*		3.4	−22.5	2.9	34,820	160	40,270–39,530	Döppes et al. 2016
17,805	Schlenken	A	1590	*U. s. eremus*	mp fragment	3.9	−35.7	0.9	22,860	90	27,990–27,150	new
14,914	Wildkirchli	CH	1420	*U. s. eremus*	mt fragment	3.3	−23.9	1.4	>49,000			new
14,911	Schwabenreith	A	959	*U. s. eremus*		3.3	−27.3	7.8	47,350	800	>49,000	Döppes et al. 2016
14,912	Schwabenreith	A	959	*U. s. eremus*		3.3	−24.6	1.7	34,010	210	39,120–38,640	Döppes et al. 2016
17,791	Schwabenreith	A	959	*U. s. eremus*		2.8	−21.8	4.9	37,400	290	42,620–41,900	Döppes et al. 2016
17,793	Schwabenreith	A	959	*U. s. eremus*		3.2	−21.7	10.5	>49,000			Döppes et al. 2016
17,795	Schwabenreith	A	959	*U. s. eremus*		2.9	−18.5	4.5	>49,000			Döppes et al. 2016
17,796	Schwabenreith	A	959	*U. s. eremus*		3.2	−20.8	0.6	48,270	930	>49,000	Döppes et al. 2016
17,797	Schwabenreith	A	959	*U. s. eremus*		3.3	−21.3	2.1	47,820	800	>49,000	Döppes et al. 2016
14,898	Herdengel	A	878	*U. s. eremus*	mp fragment	3.2	21.5	8.0	>49,000			new
14,899	Herdengel	A	878	*U. s. eremus*		3.4	−20.7	3.6	44,130	1530	46,861–44,012	Döppes et al. 2016
14,901	Herdengel	A	878	*U. s. eremus*		3.1	−23.6	2.0	45,460	370	47,628–46,532	Döppes et al. 2016
14,902	Herdengel	A	878	*U. s. eremus*		3.2	−24.0	4.0	46,510	410	48,051–47,544	Döppes et al. 2016
14,903	Herdengel	A	878	*U. s. eremus*	mp fragment	3.2	−22.5	2.9	>49,000			new
14,904	Herkova	SLO	520	*U. ingressus*	ph 1 fragment	3.9	−27.8	0.7	34,080	300	39,370–38,360	new
17,784	Winden	A	190	*U. ingressus*	mc 5	3.2	−21.0	6.1	>49,000			new
17,786	Winden	A	190	*U. ingressus*	mc fragment	3.2	−22.7	5.7	38,810	600	43,180–42,320	new
17,787	Winden	A	190	*U. ingressus*	mc 5 fragment	3.2	−16.2	10.3	45,150	590	49,300–47,550	new
17,788	Winden	A	190	*U. ingressus*	mc fragment	3.2	−24.7	5.0	30,870	110	36,130–35,010	new
17,789	Winden	A	190	*U. ingressus*	mc fragment	3.2	−20.0	5.7	42,320	310	45,850–45,280	new
17,790	Winden	A	190	*U. ingressus*	mc 5 fragment	-	−22.8	5.3	32,050	170	36,710–36,460	new

Abbrations: mand – mandible, mc – metacarpal bone, mp – metapodial bone, mt – metatarsal bone, ph 1 – basal phalanx

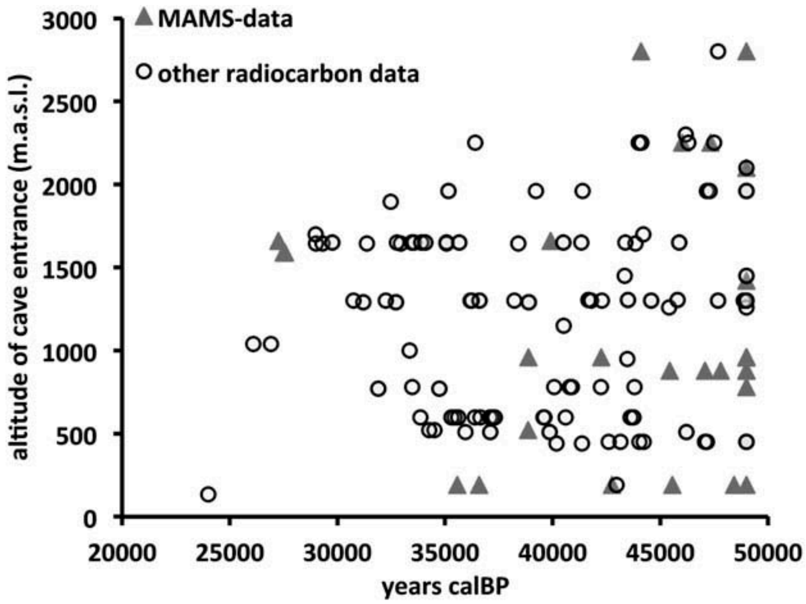

Figure 1. AMS dates of Alpine cave bears from different altitudes including the new MAMS dates (other dates are compiled from Frischauf et al. 2018) .

Sites

Conturines (Ander dles Conturines, Conturines cave) is the highest site of cave bears and cave lions (Rabeder 1991) and is located in the Gader Valley (Dolomites, South Tyrol). Most dates from this cave have given C14 ages beyond the radiocarbon range (>49 ka BP, Spötl et al. 2014, 2017). The samples were taken during the excavations 1988 to 2001.

Schreiberwand (Schreiberwand cave): This small cave is located in a vertical rock wall in the Dachstein massif, shaped by an ice-age glacier (Döppes and Rabeder 1997). The samples were taken during an excursion in 2001.

Bärenfalle (means: bear trap): This small cave is the highest cave lion site from Austria and is located in a vertical rock wall in the Tennen Mountain in the district of Salzburg near Bischofshofen, also here the glacier of the last ice age had formed this wall. The samples were taken during the excavations 2015 and 2016 (Frischauf et al. 2015).

Brettstein (Brettstein bear cave). This cave is part of the Brettstein cave system located on the karst plateau of Totes Gebirge (Döppes et al. 2016). The most recent radiocarbon dates indicate that the plateau was still ice-free at the time around 26,400 years BP. The samples were taken during the excavation campaign 1994–1997 (Döppes and Rabeder 1997).

Schlenken (Schlenken-Durchgangshöhle, Schlenken Passage Cave): The cave is located near Salzburg. The rich fossil material was recently described for the first time (Knaus et al. 2017). The samples were taken during the excavation 1979.

Wildkirchli (means: wild chapel): The Wildkirchli cave is situated in the Alpstein massif in the canton Appenzell Innerrhoden (Switzerland). The samples came from the collection of the Naturmuseum Sankt Gallen (Toni Bürgin).

Schwabenreith (Schwabenreith cave) is located near Lunz am See in the western part of Lower Austria. The fossil-rich layer is covered by a sinter blanket, which has been formed within more than 70 ka BP (Döppes and Rabeder 1997). Since new dates (Döppes et al. 2016) contradict this time frame, a solution to this problem is in progress. The samples were taken from the excavations (1993–2001).

Herdengel (Herdengel cave) is located near the Schwabenreith cave. The samples from the 3 m thick bone layer were taken from the excavations 1983 to 1989 (Döppes and Rabeder 1997).

Herkova (Jama pod Herkovimi pecmi, Herkova cave): The small cave is located close to Radlje ob Drave (Slovenia). By far the largest part of the material from this cave belongs to *U. deningeroides*, most likely from the Middle Pleistocene (Pohar et al. 2003), but there are also some younger bear remains that may belong to *U. ingressus*. The samples were taken from the excavations (2003–2005).

Winden (Ludlhöhle, bear cave of Winden): This extremely fossil-rich cave is the lowest situated bear cave in the Alps (Döppes and Rabeder 1997) and is located 50 km SE of Vienna. The samples came from the collections before 1970.

Results

New radiocarbon results

The Curt Engelhorn-Centre for Archaeometry (CEZA) received 28 samples of cave bear bones to determine the age by 14C with the MICADAS Accelerator. The radiocarbon dates are shown in Table 1.

The 14C age is normalized to δ13C = − 25 ‰ (Stuiver and Polach 1977) using the δ13C value measured in the accelerator. Its error is reported to approximately 0.5‰. However, the value can be falsified compared to the actual value of the sample by isotope fractionation during sample preparation, graphitisation and in the ion source of the accelerator (Němec et al. 2010; Wacker et al. 2010). However, the δ 13C value is tracking the actual amount of fractionation and is crucial to correct those fractionation effects to the 14C measurement. Though an important value for the 14C measurement, the d13C value is not comparable with the measurement in a mass spectrometer for stable isotopes (IRMS) and should not be used for further data interpretation. Typically, the AMS-derived value is accurate within 2–3‰ compared to the original value. Larger deviations are normal and do not signify analytical problems or low sample quality. The C/N ratios of well-preserved collagen typically shows values between 2.9 to 3.6 (DeNiro 1985) and most samples are within this range (Table 1). Only two samples (17,805 and 14,904) slightly exceed this range with a value of 3.9 and their respective ages are interpreted cautiously. The collagen preservation of the samples is sufficiently good with values from 0.6 to 13.6.

The determination of C14 ages close to the detection limit makes a careful sample preparation and measurement necessary. To check for this problem process blanks using bones of exactly known ages are pretreated and measured with our bone samples. It is general consensus of the radiocarbon labs, that ages beyond 49,000 years should not be reported with assigned ages.

Especially new dates from three sites are of great importance. First, most dates from the highest cave bear site Conturines cave has given indefinite conventional 14C-ages (>49 ka BP, Spötl et al. 2014, 2017). Regarding the ages reported by Beta-143,246 with 44,260 ± 900 years BP (Hofreiter et al. 2004) and the recently measured sample MAMS-14,895 with 40,190 ± 900 years BP (see Table 1) the cave bear must have inhabited this cave probably between 40–49 ka. Second, the five new dates from the 3 m thick bone layer of the Herdengel cave confirm a spread of approximately 5,000 years (using the minimum and the maximum range of individual dates, see Döppes et al. 2016). And last but not least, the dating of bear remains of the Winden cave, the lowest situated bear cave in the Alps. We would expect the youngest date of cave bears here in a normal course of HDEL.

HDEL (height dependent extinction line) of cave bears

An extinction line generally shows a change in the number of fossils present. If there are no remaining species, an extinction took place. An extinction line can provide clues as to why the extinction occured.

The HDEL (Height Dependent Extinction Line) shows the radiocarbon dates of alpine cave bears in relation to altitude. The recent age values lie on the HDEL which connects the points with the lowest ages per level (Figure 2).

The HDEL descends from an altitude of 2,800 m a.s.l. by about 44,840 years calBP (MAMS-14,895) to an altitude of about 1,600–1,700 m a.s.l. at 26,940 years calBP (MAMS-14,893), which can be explained by the general cooling of the climate. In the lowlands, the cave bears – according to the course of the HDEL – have disappeared much earlier (Figure 2). We offer the hypothesis that the aridity derived from Alpine foothills by the occurrence of typical steppe elements (*Mammuthus-Coelodonta*-Faunenkomplexes, Kahlke 1994) has also gradually affected the inner valleys of the Alps. The food sources of the cave bears have declined so that they have first disappeared from the lowlands and then increasing from the regions up to 1,600 m a.s.l.. The comparison of stable carbon and nitrogen isotopes as well as the different frequencies of grinding marks allows conclusions about the composition of nutrition at different altitude levels (Bocherens et al. 2011; Horacek et al. 2012; Krajcarz et al. 2016).

There is no evidence for the hypothesis that the Paleolithic man had influenced the extinction of the Alpine cave bear.

The geological youngest cave bears of the alps

The new dates complete the recently published extinction pattern (Rabeder et al. 2017a). Almost all geological most

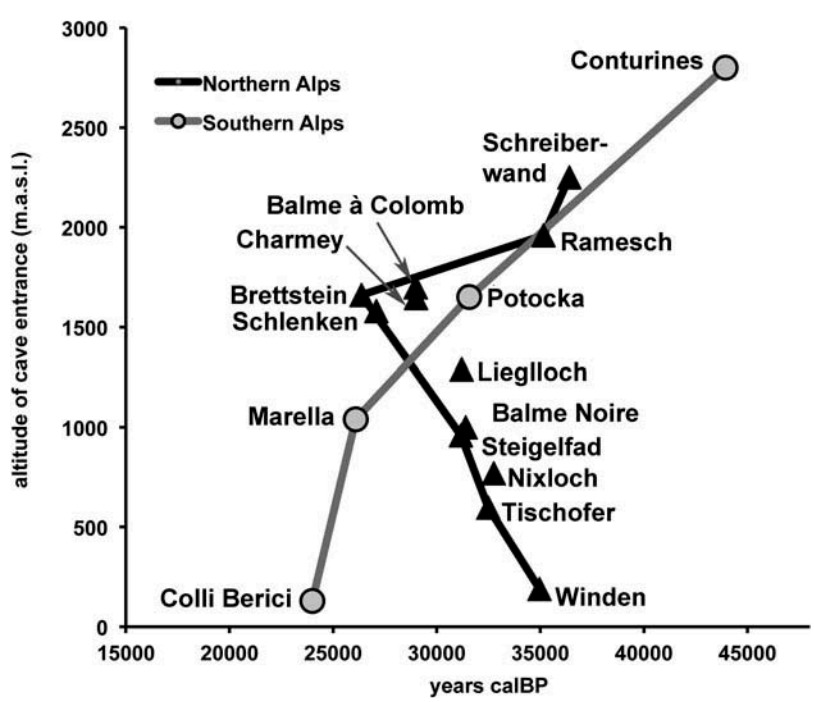

Figure 2. The most recent Alpine cave bear dates according to (Argant and Argant 2004; Blant et al. 2010; Bocherens et al. 2011; Bolus and Conard 2006; Bona 2004; Castel et al. 2010; Döppes et al. 2011, 2012, 2016; Döppes and Rabeder 1997; Frischauf 2011; Hille and Rabeder 1986; Imhof (pers. Comm). 2014; Pacher and Stuart 2009; Perego et al. 2001; Rabeder 1995; Spötl et al. 2014; Terlato et al. 2018) and this paper.

recent AMS dates of Alpine cave bears are from altitudes between 1500 to 1700 m above sea level. This applies in the same way to the Western Alps and the Eastern Alps, the Northern and the Southern Alps. The AMS dates from the caves in lower altitudes have higher values.

But there is one exception: In Grotta sopra Fontana Marella two datings (26,090 and 26,919 years calBP, ETH-5198 and ETH-5199, Perego et al. 2001) are in the same time range, but the cave is located in an altitude of only 1,040 m a.s.l..

It is still too early to assert that the course of the climate south of the main Alpine crest was essentially different from the climate in the Northern Alps. But new dates (Terlato et al. 2018) strengthen this assumption: several radiocarbon dates from cave bears from caves of the Colli Berici lie around 24,000 years calBP and suggest that the climate south of the Alps was not as dry as in the north. We hope to get new data from the numerous bear caves in Northern Italy to confirm or refute this hypothesis.

Taxonomy and extinction

The extinction of cave bears in the Alps was obviously different than in the lowlands. While e.g. in the Ach Valley (Germany, 534 m a.s.l. see Münzel et al. 2011) the populations of *U. s. eremus* disappeared more than 1,000 years earlier than *U. ingressus*, we have a completely different pattern of extinction in the Alps: *U. spelaeus eremus* inhabited in the high Alps several thousand years longer than *U. ingressus* (see Figure 3). However, the most recent date of *Ursus ingressus* comes from the low laying areas of Colli Berici (Italy, see poster presentation at the International Cave Bear Symposium 2017 by Christian Urban, Joscha Gretzinger, Ella Reiter, Hervé Bocherens, Martin Sabol, Verena J. Schuenemann and Johannes Krause).

U. ladinicus has disappeared from the Alps more than 40,000 years calBP ago.

Geographic distribution of the youngest 14C date

The geographical distribution of the caves with the most recent age information is scattered throughout the Alps (Figure 3). It can be surmised that the main reason for the extinction of the cave bears was the general cooling associated with the incipient cold phase of the Würmian glacial.

Course of HDEL (height dependent extinction line)

Almost all caves with the most recent AMS dates are in an altitude level between 1,500 and 1,700 m a.s.l.. This zone must have been particularly climatically favoured: high summer temperatures coupled with sufficient rainfall allowed the bears to survive in this altitude while in deeper areas of the Northern Alps the precipitation was too low for suitable plant nutrition. The dates from the Grotta sopra Fontana Marella

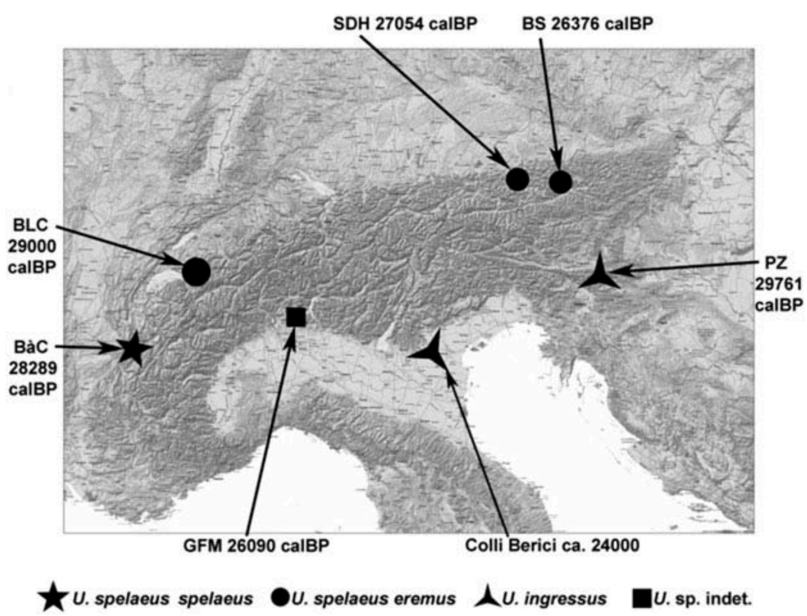

Figure 3. Geographic position of caves with the current youngest cave bear 14C dates in the Alpine region (see Table 2).

Table 2. Current youngest cave bear 14C dates in the Alpine region.

abbreration	cave name	state	altitude (m)	C14_age (years BP)	cal BP (1-σ)	references
BàC	Balme à Colomb	F	1700	24,160 ± 370	28,560–27,860	Argant and Argant 2004
BLC	Bärenloch near Charmey	CH	1645	24,175 +/- 365	28,570–27,870	Blant et al. 2010
BS	Brettstein cave	A	1660	22,510 +/-120	27,580–26,940	Döppes et al. 2016
CB	Colli Berici: Paina cave	I	350	19,686 +/-54	23,830–23,600	Terlato et al. 2018
CB	Colli Berici: Trene cave	I	360	19,948 +/-55	24,108–23,900	Terlato et al., 2018
GFM	Grotta sopra Fontana Marella	I	1040	21,810 +/-200	26,230–25,850	Perego et al., 2001
PZ	Potocka zijalka	SLO	1650	26,900 +/-110	31,110–30,910	Pacher and Stuart 2009
SDH	Schlenken-Durchgangshöhle	A	1590	22,860 +/- 90	27,990–27,150	new

and from the Colli Berici form an enigmatic exception which can be explained by the assumption that the climate in the Southern Alps was much more humid.

Conclusions and discussion

Based on pollen findings in cave sediments (Hille and Rabeder 1986), isotope examinations (e.g. Bocherens et al. 2011; Horacek et al. 2012) as well as abrasion of the teeth (e. g. Frischauf et al. 2016) it could be confirmed over the decades that cave bears fed almost exclusively on herbs and leaves. It was assumed that with the general cooling in the OIS 3 since about 45 ka also the migration of the alpine elements into the lowlands took place and the food of the cave bears in intermediate altitudes consisted mainly of relatively soft plants (herbs, leaves), while cave bears in lower altitudes had to accept a higher proportion of hard plants (grasses). The expectation of HDEL that the oldest finds can be found in the higher alpine altitudes and the youngest in the lowlands has not been confirmed.

The new radiocarbon dates have consolidated the course of HDEL for the Northern Alps. The cave bears have survived the longest at an altitude between 1,500 and 1,700 m a.s.l., while they disappeared earlier from caves in lower areas. While the lowering of HDEL from 2,300 m a.s.l. (about 45,000 years ago) to 1,500–1,700 m a.s.l. (26,000 years ago) can be explained by the general cooling of the climate, the peculiar lowering of the HDEL – the lower the location of the caves the sooner the disappearance of the cave bears – can be explained by the increasing aridity that created steppes at the Alpine foothills.

Possibly the HDEL was different in the Southern Alps. The lowering of the HDEL occurred in the same direction with the decrease of the altitude. The climate was not as affected by the decrease in precipitation as in the northern Alps: the cave bears disappeared here more than 2,500 years later.

It can be concluded that a general cooling at the beginning of the Last Glacial Maximum (LGM) lead to the extinction of the cave bear in the Alps and the cave bear became extinct in the middle of the long cold stadial GS-3 (Baca et al 2016). It could be recognized that the populations in the lower situated cave bear site became earlier extinct than the cave bear population in the higher altitudes (around 1,500 m a.s.l.).

An explanation would be a steppe environment at the foothills and Alpine valleys caused by the Heinrich events or the assumed south weather situation in the LGM (Wohlfarth et al. 2008).

Acknowledgments

We thank the technical personal of the CEZA radiocarbon lab for the great care taken during sample preparation and testing of the pre-treatment procedures. The authors are grateful for the helpful comments and the constructive suggestions of the two anonymous reviewers.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Argant A, Argant J. 2004. Datations et environnement des ours de Bâlme à Collomb (Entremont-le-Vieux, Savoie, France). Cah Sci Mus Hist Nat Lyon Hors-Série. 2:189–197.

Baca M, Popović D, Stefaniak K, Marciszak A, Urbanowski M, Nadachowski A, Mackiewicz P. 2016. Retreat and extinction of the Late Pleistocene cave bear (*Ursus spelaeus* sensu lato). Sci Nat. 103 (11):92.

Blant M, Bocherens H, Bochud M, Braillard L, Constandache M, Jutzet JM. 2010. Le gisement à faune Würmienne du Bärenloch (Préalpes fribourgeoises). Bull Soc Frib Sci Nat. 99:1–22.

Bocherens H. 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quat Sci Rev. 117:42–71.

Bocherens H, Stiller M, Hobson KA, Pacher M, Rabeder G, Burns JA, Tütken T, Hofreiter M. 2011. Niche partitioning between two sympatric genetically distinct cave bears (*Ursus spelaeus* and *Ursus ingressus*) and brown bear (*Ursus arctos*) from Austria: isotopic evidence from fossil bones. Quat Int. 245:238–248.

Bolus M, Conard NJ. 2006. Zur Zeitstellung von Geschossspitzen aus organischen Materialien im späten Mittelpaläolithikum und Aurignacien. Arch Korrespondenzblatt. 36(1):1–15.

Bona F. 2004. Preliminary analysis on *Ursus spelaeus* Rosenmüller et Heinroth, 1794 populations from „Caverna Generosa“ (Lombardy – italy). Cah Sci Mus Hist Nat Lyon Hors-Série. 2:87–98.

Castel JC, Oppliger J, Luret M, Pacher M, Wildberger A, Jörin U, Bourret F. 2010. Nouvelles données sur les populations d'*Ursus spelaeus* et d'*Ursus arctos* de la Geissbachhöhle (Ennanda, Glaris, Suisse). Quaternaire. 4:127–136.

DeNiro MJ. 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. Nature. 317:806.

Döppes D, Pacher M, Frischauf C, Rabeder G. 2012. New scientific results from the Arzberg Cave near Wildalpen, Styria, Austria. Braunschw Naturk Schr. 11:41–48.

Döppes D, Pacher M, Rabeder G, Lindauer S, Ronny F, Kromer B, Rosendahl W. 2016. Unexpected! New AMS datings from Austrian cave bear sites. Cranium. 33(1):26–30.

Döppes D, Rabeder G. 1997. Pliozäne und pleistozäne Faunen Österreichs Ein Katalog der wichtigsten Fossilfundstellen und ihrer Faune. Mitt Komm Quartärforsch Österr Akad Wiss. 10:1–411.

Döppes D, Rabeder G, Stiller M. 2011. Was the middle Würmian in the high Alps warmer than today? Quat Int. 245:193–200.

Figueirido B, Palmqvist P, Pérez-Claros JA. 2009. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics. J Zool. 277:70–80.

Frischauf C 2011. Die Ochsenhalthöhle im Toten Gebirge (Steiermark). Unpub. Master thesis. Univ. Vienna.

Frischauf C, Krutter S, Rabeder G. 2015. Die fossile Höhlenfauna der Bärenfalle im Tennengebirge. In: Krutter S, Schröder F, Eds. Durch die Schichten der Zeit! Neue Erkenntnisse zwischen Mesozoikum und Gegenwart (Festschrift für Erich Urbanek zum 75. Geburtstag). Golling: Forschungen des Museums Burg Golling; p. 33–44.

Frischauf C, Gockert R, Kavcik-Graumann N, Rabeder G. 2016. "Kiskevély knifes" indicate the menu of Alpine cave bears - Comparative studies on wedge shaped defects of canines and incisors. Cranium. 33:14–17.

Frischauf C, Nielson E, Rabeder G. 2018. The cave bear fauna (Ursidae, Mammalia) from Steigelfadbalm near Vitznau. Canton of Lucerne (Switzerland): Acta Zoologica Cracoviensia (in press).

Hille P, Rabeder G. 1986. Die Ramesch-Knochenhöhle im Toten Gebirge. Mitt Komm Quartärforsch Österr Akad Wiss. 6:1–66.

Hofreiter M, Rabeder G, Jaenicke-Després V, Withalm G, Nagel D, Paunovic M, Jambrešic G, Pääbo S. 2004. Evidence for reproductive isolation between cave bear populations. Curr. Biol.14(1):40–43.

Horacek M, Frischauf C, Pacher M, Rabeder G. 2012. Stable isotopic analyses of cave bear bones from the Conturines Cave (2,800 m, South Tyrol, Italy). Braunschw Naturk Schr. 11:49–54.

Jones DB, DeSantis LR. 2016. Dietary ecology of the extinct cave bear: evidence of omnivory as inferred from dental microwear textures. Acta Palaeontol Polonica. 61(4):735–741.

Kahlke RD. 1994. Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des oberpleistozänen *Mammuthus-Coelodonta*-Faunenkomplexes in Eurasien (Grosssäuger). Abh Senckenberg naturfoIsch Ges. 546:1–164.

Knaus T, Schopf B, Frischauf C, Kavcik-Graumann N, Rabeder G. 2017. The cave bears from Schlenken-Durchgangshöhle (Schlenken Passage Cave Osterhorn Massif, Salzburg, Austria). Aragonit. 22(1):13–14.

Krajcarz M, Pacher M, Krajcarz MT, Laughlan L, Rabeder G, Sabol M, Wojtal P, Wojtal H. 2016. Isotopic variability of cave bears (d 15N, d 13C) across Europe during MIS 3. Quat Sci Rev. 131:51–72.

Münzel S, Stiller M, Hofreiter M, Mittnik A, Conard NJ, Bocherens H. 2011. Pleistocene bears in the Swabian Jura (Germany): genetic replacement, ecological displacement, extinctions and survival. Quat Int. 245:225–237.

Němec M, Wacker L, Gäggeler H. 2010. Optimization of the Graphitization process at Age-1. Radiocarbon. 52(3):1380–1393.

Pacher M, Stuart AJ. 2009. Extinction chronology and palaeocology of the cave bear (*Ursus spelaeus)*. Boreas. 38:189–206.

Perego R, Zanaldi E, Tintori A. 2001. *Ursus spelaeus* from Grotta supra Fontana Marella, Campo di Fiori Massiv (Varese, Italy): morphometry and Palaeoecology. Rev. Ital. Pal. 107:451–462.

Pohar V, Debeljak I, Rabeder G 2003. Cave bear site Jama pod Herkovina pecmi (N. Slovenia): preliminary study. 9ème Symposium International Ours des Cavernes, Savoie (France) : Entremont-le-Vieux, Abstracts, p. 70.

Rabeder G. 1991. Die Höhlenbären von Conturines. Entdeckung und Erforschung einer Dolomiten-Höhle in 2800 m Höhe. Bozen: Athesia.

Rabeder G. 1995. Die Gamssulzenhöhle im Toten Gebirge. Mitt Komm Quartärforsch Österr Akad Wiss. 9:1–133.

Rabeder G, Döppes D, Frischauf C, Kavcik-Graumann N, Kromer B, Lindauer S, Friedrich R, Rosendahl W. 2017a. Extinction pattern of Alpine cave bears New Data and Climatological Interpretation. Aragonit. 22(1):21.

Rabeder G, Frischauf C, Nielsen E. 2017b. Steigelfadbalm, eine fossilführende Bärenhöhle in der Nagelfluh der Rigi bei Luzern (Zentralschweiz). Die Höhle. 68:124–133.

Robu M, Fortin JK, Richards MP, Schwartz CC, Wynn JG, Robbins CT, Trinkaus E. 2013. Isotopic evidence for dietary flexibility among European Late Pleistocene cave bears (*Ursus spelaeus*). Can J Zool Rev. 91:227–234.

Spötl C, Reimer P, Rabeder G, Bronk RC. 2017. Radiocarbon Constraints on the Age of the World's Highest-Elevation Cave-Bear Population, Conturines Cave (Dolomites, Northern Italy). Radiocarbon. 1–9. doi:10.1017/RDC.2017.60

Spötl C, Reimer PJ, Rabeder G, Scholz D. 2014. Presence of cave bears in western Austria prior to the onset of the Last Glacial Maximum: new radiocarbon dates and palaeoclimatic considerations. J Quat Sci. 29 (8):760–766.

Stiller M, Molak M, Prost S, Rabeder G, Baryshnikov G, Rosendahl W, Münzel S, Bocherens H, Grandal-d'Anglade A, Hilpert B, et al. 2014. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. Quat. Int. 339–340:224–231.

Stuiver M, Polach HA. 1977. Discussion: reporting of 14C data. Radiocarbon. 19:355–363.

Terlato G, Bocherens H, Romandini M, Nannini N, Ka H, Peresani M. 2018. Chronological and Isotopic data support a revision for the timeing of cave bear extinction in Mediterranean Europe. Hist Biol. 1–11. doi:10.1080/08912963.2018

Wacker L, Bonani G, Friedrich M, Hajdas I, Kromer B, Němec M, Vockenhuber C. 2010. MICADAS: routine and high-precision radiocarbon dating. Radiocarbon. 52(2):252–262.

Wohlfarth B, Veres D, Ampel L, Lacourse T, Blaauw M, Preusser F, Andrieu-Ponel V, Keravis D, Lallier-Verges E, Bjorck S, et al. 2008. Rapid ecosystem response to abrupt climate changes during the last glacial period in western Europe, 40–16ka. Geology. 36:407–410.