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Extinction chronology of the cave lion *Panthera spelaea*

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ABSTRACT

The cave lion, *Panthera spelaea*, was widespread across northern Eurasia and Alaska/Yukon during the Late Pleistocene. Both morphology and DNA indicate an animal distinct from modern lions (probably at the species level) so that its disappearance in the Late Pleistocene should be treated as a true extinction. New AMS radiocarbon dates directly on cave lion from across its range, together with published dates from other studies – totalling 111 dates – indicate extinction across Eurasia in the interval ca. 14–14.5 cal ka BP, and in Alaska/Yukon about a thousand years later. It is likely that its extinction occurred directly or indirectly in response to the climatic warming that occurred ca. 14.7 cal ka BP at the onset of Greenland Interstadial 1, accompanied by a spread of shrubs and trees and reduction in open habitats. Possibly there was also a concomitant reduction in abundance of available prey, although most of its probable prey species survived substantially later. At present it is unclear whether human expansion in the Lateglacial might have played a role in cave lion extinction. Gaps in the temporal pattern of dates suggest earlier temporary contractions of range, ca. 40–35 cal ka BP in Siberia (during MIS 3) and ca. 25–20 cal ka BP in Europe (during the 'Last Glacial Maximum'), but further dates are required to corroborate these. The Holocene expansion of modern lion (*Panthera leo*) into south-west Asia and south-east Europe re-occupied part of the former range of *P. spelaea*, but the Late Pleistocene temporal and geographical relationships of the two species are unknown.

1. Introduction

Lions (*Panthera leo* (L.)) are today restricted to Sub-Saharan Africa, with an isolated population of Asiatic lion in the Gir Forest National Park and Wildlife Sanctuary in north-west India. In the late Pleistocene, however, 'cave lions' ranged across most of Europe and northern Asia and into Alaska and the Yukon. In this paper we present the first attempt to chart the chronological distribution of cave lion in the Late Pleistocene. The dataset is rather small, which reflects the rarity of available material of cave lion when compared with some other megafaunal species, such as woolly mammoth and woolly rhinoceros. However, we consider that there are sufficient data points to give a reasonable impression of the Late Pleistocene chronology of the cave lion across northern Eurasia and north-west North America (Fig. 1).

The European 'cave lion' was named *Panthera spelaea* (Goldfuss, 1810), although it has commonly been regarded as a subspecies, *P. l. spelaea* (e.g. Kurtén, 1968, 1985; Hemmer, 1974; Turner, 1984). Recent studies show that it is morphologically distinct from the living *P. leo* (Spassov and Iliev, 1994; Sotnikova and Nikolskiy, 2006), with differences in cranial and dental anatomy which Sotnikova and Nikolskiy (2006) regard as sufficient to justify specific status. For example, *P. spelaea* shows markedly more inflated bullae and braincase, more strongly arched zygomata, and P^4s (carnassials) with preparastyles, whereas *P. leo* has a relatively wider and shorter muzzle and greater width across the mastoids. Both differ significantly from the tiger *Panthera tigris*.

In North America, most authors (summarised in Sotnikova and Nikolskiy, 2006) have agreed that the lion of eastern Beringia (Alaska/Yukon) is to be equated with *spelaea*, but pantherine cats south of the Late Pleistocene Laurentide ice sheet have been distinguished as *Panthera atrox* (Leidy, 1853) at either the specific level (Sotnikova and Nikolskiy, 2006), or as a subspecies *P. l. atrox* (Kurtén, 1968, 1985; Hemmer, 1974; Turner, 1984).

The taxonomic distinction of the cave lion from living lions has been confirmed by a pioneer study of ancient and modern DNA (Burger et al., 2004) and by a recent, more detailed study (Barnett et al., 2009) which found that the lions of the Late Pleistocene and Holocene fall into three distinct groups: (1) the living African and Asian lions; (2) the extinct cave lion, and (3) the extinct American lion. These studies confirm the referral of Beringian populations (east and west) to *spelaea*, but do not find any mtDNA

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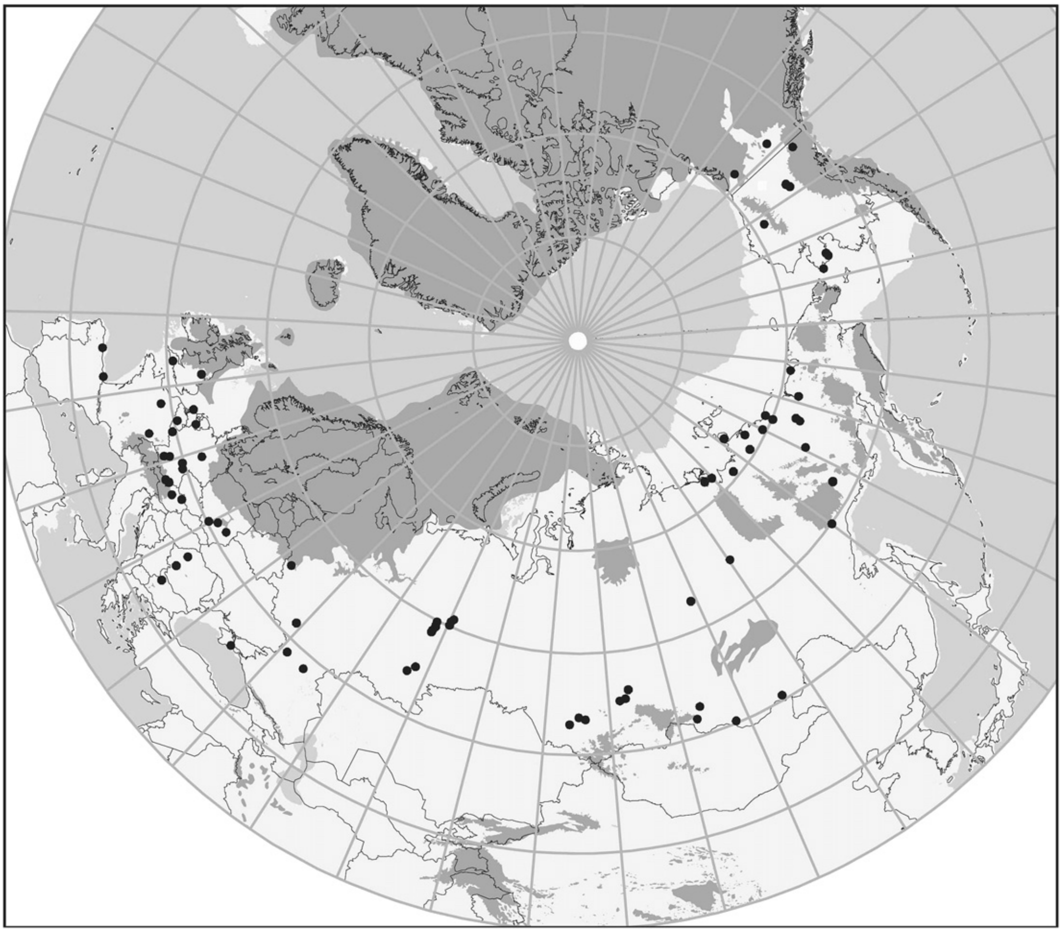

Fig. 1. Map of ^{14}C-dated records of cave lion *Panthera spelaea* (data from Table 1). LGM ice limits from Ehlers and Gibbard (2004a–c). The sea level is shown schematically at 100 m below that of the present day.

evidence for their differentiation from other *spelaea* populations, in spite of their having been named *Panthera s. vereschagini* on morphological grounds by Baryshnikov and Boeskorov (2001).

The status of *P. atrox* is uncertain. Most authors have assumed it to be derived from early populations of *P. spelaea*, the characters distinguishing *atrox* being seen as mainly derived with respect to *spelaea* (Sotnikova and Nikolskiy, 2006). Christiansen (2008) and Christiansen and Harris (2009), however, do not consider *atrox* a lion at all, but a late offshoot of the American jaguar lineage which entered the continent in the Early Pleistocene. This view is not supported by the mtDNA data, which suggest that *atrox* was derived from a Beringian population of *spelaea* that dispersed into North America and was subsequently isolated, the most recent common ancestor of the two being estimated at around 337 kyr BP (Barnett et al., 2009). However, the authors recognise that larger samples, and the addition of nuclear DNA, are required to confirm this conclusion. This issue is beyond the scope of the present paper.

Whatever their precise taxonomic status, it is clear that *spelaea* and *atrox* were entities distinct from modern lions and from each other. Their respective disappearances are therefore to be treated as extinctions, rather than merely the extirpation of an (albeit very large) part of the distribution of a modern taxon (Lister and Stuart, 2008). They thus form part of the major global episode of megafaunal extinctions that occurred within the last Glacial–Interglacial cycle (Martin and Steadman, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006). As we have shown in previous papers (Stuart, 1991, 1999; Martin and Stuart, 1995; Stuart and Lister, 2007) in northern Eurasia the extinctions were staggered over tens of millennia, contrasting with an apparently much sharper pulse of extinctions in North America.

By the same token, the Late Quaternary history of the modern lion, *P. leo*, can be regarded as a topic distinct from that of *P. spelaea* or *P. atrox*. According to written accounts, within the past 200 years the Asiatic lion ranged from North Africa, through Iraq, and Turkey to Iran, Pakistan and north-west India (Bartosiewicz, 2009), and there are sporadic records from some of these areas from the first half of the twentieth century. The decline of these populations was probably initiated by hunting in the ancient world evidenced, for example, by Assyrian low-relief sculptures graphically depicting lion hunts (http://www.britishmuseum.org/research/search_the_collection_database.aspx), and especially by the large-scale capture of animals for the arena in Roman times. More recently, in the last two centuries, the Asiatic lion was brought to the verge of extinction largely by hunting with firearms.

2. Palaeobiology

The Late Pleistocene cave lion was exceptionally widely distributed, ranging from Britain and Iberia across most of northern Eurasia (Kahlke, 1994), and into Alaska and the Yukon (Fig. 1), with the American lion *P. atrox* replacing it to the south in the USA and southern Canada. However, it was absent from Ireland, Fennoscandia, north-west Siberia and Taimyr: the reason for its absence from the latter is unclear since suitable prey, including horse, bison

Table 1
List of radiocarbon dates on cave lion *Panthera spelaea* and American lion *Panthera atrox.*

	Country	Region	Site	Lab code	^{14}C date	Error	Material dated	Cal plus	Cal minus	Cal median	latDD	longDD	Delta ^{13}C	CN	Source
Panthera spelaea															
1	Spain	Asturias	Jou'l Llobu	OxA-10186	46,400	2100	Metatarsal	52,108	44,872.5	48,550	43.3	−5.8	−18.081	3.4	This paper
2	Spain	Cantabria	Urtiaga Cave	OxA-10121	13,770	120	Astragalus	17,395	16,935	17,032	43.28	−2.315	−18.16	3.4	This paper
3	Bulgaria	North-west Sofiya region	Lakatnik Cave	OxA-11422	31,200	330	Metatarsal III	35,910	34,964.5	35,397	43.05	23.4	−17.367	3.3	This paper
4	Romania	Bihor County	Ursilor Cave	OxA-22122	39,000	1000	Upper incisor I1 (from skull)	43,552	41,223	42,033	46.55	22.57	−18.51	3.2	This paper
5	Romania	Bihor County	Ursilor Cave	OxA-22123	38,600	1000	Upper incisor I3 from associated skeleton	43,542	40,945	41,816	46.55	22.57	−17.67	3.2	This paper
6	Romania	Gorj	Closani Cave	OxA-22124	33,150	500	Left mandible	40,088	35,990	37,974	45.08	22.80	−18.74	3.3	This paper
7	Romania	Gorj	Closani Cave	OxA-22125	32,500	450	Left mandible	39,089	35,622	36,986	45.08	22.80	−18.77	3.3	This paper
8	Britain	Devon	Kent's Cavern	OxA-14285	43,600	3600	Left upper canine	52,177.5	42,115.5	47,974	50.468	−3.532	−17.4		R. Jacobi (pers. comm.)
9	Britain	Derbyshire	Pin Hole Cave, Creswell Crags	OxA-19092[a]	35,650	450	Scapula	41,192	39,426	40,626	53.263	−1.204	−19.174	3.2	This paper
10	Netherlands	Gelderland	Lathum	OxA-16715	44,850	650	Left mandible	48,829	43,927	45,533	51.99	6.02	−19.1	3.2	This paper
11	Netherlands	North Sea	Eurogeul	GrA-23151	42,230	570	Ulna	44,865	42,052	43,692	52.02	3.82			Mol et al. (2006)
12	Luxembourg	Luxembourg	Altwies	KIA-4944	31,690	500	Pelvis	38,013	34,946	35,999	49.51	6.257			Baales and Le Brun-Ricalens (1996)
13	Belgium	Namur	Trou Magrite	OxA-6593	25,980	340	1st Phalanx	30,070	29,375	29,717	50.22	4.9			Charles et al. (2003)
14	France	Jura	Abri des Cabones, Ranchot	OxA-12021	12,565	50	Canine	15,032	14,614	14,880	47.151	5.726	−18.1	3.2	This paper
15	France	Paris	Le Closeau	AA-41882 [2]	12,248	66	Metacarpal V	14,606	13,675	14,141	48.873	2.154			Bodu and Mevel (2008)
16	Germany	Swabian Alb	Sybillenhöhle	OxA-15354	>48,100		Calcaneum	NC	NC	NC	48.649	9.408	−18.4		Barnett et al. (2009)
17	Austria	Ober-österreich	Gamssulzen Höhle	OxA-13110	49,900	1500	Tibia	58,396	47,845	52,042	47.682	14.299	−19.205		Barnett et al. (2009)
18	Germany	Franconian Alb	Zoolithen-höhle	OxA-14863	47,600	900	Phalanx	52,110	45,990	48,877	49.551	11.6	−18.7		Barnett et al. (2009)
19	Germany	Bavaria	Siegsdorf	KIA-14406	47,180	1190	Bone from skeleton	58,179	44,907	48,557	47.823	12.647	−19.4		Burger et al. (2004)
20	Austria	Nieder-österreich	Teufelslucke	VERA-2545	42,400	1800	Premolar P4	52,095	41,805	44,395	48.67	40.856			M. Pacher (pers. comm.)
21	Poland	Krakow-Czestochowa Upland	Zawalona Cave	OxA-11156	38,800	1100	R premolar P4	42,549	41,300.5	41,958	50.07	19.72	−18.404	3.3	This paper

(*continued on next page*)

Table 1 (*continued*)

	Country	Region	Site	Lab code	^{14}C date	Error	Material dated	Cal plus	Cal minus	Cal median	latDD	longDD	Delta ^{13}C	CN	Source
22	Poland	Krakow-Czestochowa Upland	Wierchowska Gorna	OxA-10087	38,650	600	Bone	41,926.5	41,395.5	41,711	51.13	22.28	−18.2		Barnett et al. (2009)
23	Germany	Bavaria	Baumanns-höhle	Erl-6209	34,645	365	Femur	40,727	38,635	39,816	51.755	10.843			Rosendahl et al. (2005)
24	Austria	Tirol	Tischofer-höhle	KIA 16510	31,890	300	Pelvis	37,981	34,972	36,186	47.583	12.167			Burger et al. (2004)
25	Germany	Franconian Alb	Gremsdorf	OxA-14862	28,310	50	Femur	32,521.5	31,105.5	31,723	42.82	10.82	−17.9		Barnett et al. (2009)
26	Poland	Świętokrzyskie Province	Raj Cave	OxA-11096	25,190	350	Atlas	29,597.5	28,715	29,138	50.83	20.5	−18.936	3.4	This paper
27	Austria	Niederösterreich	Schusterlucke Cave	OxA-10513	15,400	130	Phalanx	19,189	17,945	18,521	48.451	15.403	−19.6	3.6	This paper
28	Germany	Baden-Württemberg	Zigeunerfels Cave	OxA-17268	12,375	50	Upper canine	14,851	14,095.5	14,378	48.0858	9.156	−18.38	3.1	This paper
29	Ukraine	Crimea	Emine-Bair-Khosar Cave	OxA-17044	56,400	2100	Metatarsal	NC	NC	NC	45	35	−18.36	3.2	This paper
30	Ukraine	Crimea	Emine-Bair-Khosar Cave	OxA-17045	>60,200		Metatarsal (repeat)	NC	NC	NC	45	35	−18.18	3.2	This paper
31	Russia	European Russia	Volga-Don Canal	OxA-17031	28,480	200	Femur	32,887	31,171	32,173	48.5	44	−17.60	3.2	This paper
32	Russia	European Russia	Kostenki I	OxA-17372	23,400	100	Metatarsal IV	27,230	26,904.5	27,058	51.4	39	−16.92	3.3	This paper
33	Russia	European Russia	Kostenki I	OxA-17032	23,190	120	Metacarpal III	27,181.5	26,655	26,947	51.4	39	−17.63	3.1	This paper
34	Russia	European Russia	Kostenki IV	OxA-17042	23,080	100	Maxilla, palate	26,975.5	26,608.5	26,812	51.4	39	−18.24	3.2	This paper
35	Russia	European Russia	Smolensk region	OxA-17034	14,055	60	Skull	17,459	17,058.5	17,320	54.8	32	−17.71	3.3	This paper
36	Russia	Urals	Tain Cave	OxA-10888	>49,600		Pelvis	NC	NC	NC	59.42	57.77	−18.653	3.3	This paper
37	Russia	Urals	Pobeda Cave	OxA-10845	>39,800		Humerus	NC	NC	NC	54.17	56.85	−18.382	3.2	This paper
38	Russia	Urals	Grotto Shaitansky	OxA-10907	54,500	2600	Metacarpal IV	NC	53,884	55,711	60.7	60.37	−18.106	3.2	This paper
39	Russia	Urals	Ignatievskaya Cave	OxA-10887	41,900	1200	Metatarsal III	44,493.5	42,080.5	43,513	54.9	57.78	−17.401	3.3	This paper
40	Russia	Urals	Grotto Cheremuhovo 1–2	OxA-10895	30,140	240	Phalanx-1st	34,930.5	34,490	34,643	60.4	60.05	−18.095	3.2	This paper
41	Russia	Urals	Grotto Cheremuhovo 1–1	OxA-10894	29,120	230	Metacarpal II	33,950.5	32,991.5	33,469	60.04	60.05	−17.589	3.2	This paper
42	Russia	Urals	Grotto Holodny	OxA-10910	14,750	70	Scapho-lunar	18,348.5	17,665	17,864	58.67	57.57	−18.129	3.3	This paper
43	Russia	Urals	Grotto Viasher 2	OxA-10908	13,570	70	Vertebra	17,019.5	16,874	16,926	59.8	57.67	−17.922	3.3	This paper
44	Russia	Urals	Grotto Verhnequ-bahinsky	OxA-10909	13,560	70	Scapula	17,019	16,860.5	16,916	58.87	57.6	−17.811	3.2	This paper
45	Russia	Urals	Podsemnich Ochotnikov	OxA-11349	13,500	65	Mandible	17,004.5	16,217	16,844	59.3	57.83	−17.113	3.3	This paper
46	Russia	S central Siberia	Priobskoye Steppe Plateau	OxA-16981	52,800	1600	Ulna	59,088.5	52,925.5	55,102	53	83.5	−18.93	3.1	This paper
47	Russia	Altai	Chumysh River, Zarinsk District	OxA-17043	51,400	1200	Mandible	58,834	50,316.5	53,758	53.7	84.9	−18.16	3.2	This paper
48	Russia	C Siberia	Nizhnyaya Tunguska River	OxA-16980	50,500	1300	Ulna	58,529	47,988	52,785	62.9	108.5	−17.94	3.1	This paper
49	Russia	C Siberia	Tyung	OxA-17010	46,700	1300	Femur	51,873.5	45,127	48,181	64.6	120	−17.96	3.3	This paper
50	Russia	S central Siberia	Derbina IV 2001	OxA-20252	35,750	400	Mandible	41,202	39,518	40,683	55.3	92.47	−18.44	3.2	This paper
51	Russia	S central Siberia	Derbina IV 2001	OxA-20257	35,390	280	R mandible (no teeth)	40,958	39,397	40,481	55.3	92.47	−18.17	3.2	This paper
52	Russia	Kranoyarsk Region	Kurtak 4	OxA-17373	25,700	130	Part skull, P4	29,890	29,332	29,598	55.15	91.54	−16.66	3.3	This paper

53	Russia	S central Siberia	Togul River Basin	OxA-18711	22,080	80	Femur	26,153	25,198	25,682	53.488	85.922	−18.02	3.1	This paper
54	Russia	S central Siberia	Volchika II, 2002	OxA-20251	20,085	80	Humerus	23,492	22,916	23,266	55.3	92.47	−17.87	3.2	This paper
55	Russia	S central Siberia	Kubekovo, Krasnoyarskiy Kray	OxA-17054	17,915	70	Metatarsal	21,250.5	20,212	21,034	56.149	93.113	−17.82	3.1	This paper
56	Russia	Transbaikalia	no exact locality	OxA-18712	40,210	350	Ulna	43,565	41,880	42,518	50.3	107.9	−18.22	3.1	This paper
57	Russia	Baikal, Irkutsk	Mal'ta	OxA-17033	21,500	100	Metapodial	25,118	24,218.5	24,910	52.9	103.6	−17.17	3.3	This paper
58	Russia	Baikal	Elovka	OxA-20672	18,350	75	Radius	22,014	20,510	21,634	51.789	102.666	−17.06	3.4	This paper
59	Russia	Transbaikalia	Onon River	OxA-16982	17,910	75	Radius	21,248	20,207.5	21,024	50.58	115.4	−17.65	3.1	This paper
60	Russia	NE Yakutia	Khomus-Yuryakh Bol. River	OxA-17036	>62,400		Maxilla	NC	NC	NC	70.06	153.49		3.1	This paper
61	Russia	New Siberian Islands	Bolshoi Liakhovsky Island	OxA-17039	>62,100		Metapodial	NC	NC	NC	73.36	141.33	−19.77	3.1	This paper
62	Russia	New Siberian Islands	Bolshoi Liakhovsky Island, shore 1998	OxA-13837	>62,100		Tibia	NC	NC	NC	73.32	141.37	−19.2		Barnett et al. (2009)
63	Russia	NE Yakutia	Duvannyy Yar, 1976	OxA-13829	>61,500		Femur	NC	NC	NC	68	156	−19.0		Barnett et al. (2009)
64	Russia	New Siberian Islands	Bolshoi Liakhovsky Island, in situ 1998	OxA-13836	>60,700		Bone	NC	NC	NC	73.32	141.37	−19.3		Barnett et al. (2009)
65	Russia	NE Yakutia	Stanchikovskiy Yar	OxA-17030	>58,100		Mandible	NC	NC	NC	68.37	161.5	−18.18	3.3	This paper
66	Russia	NE Siberia	Sededema River, Loc. 527	OxA-17057	>56,800		Humerus	NC	NC	NC	66.07	150.46	−19.73	3.1	This paper
67	Russia	NE Yakutia	Kolyma River, Vetrenny Creek	OxA-17029	>55,400		Mandible	NC	NC	NC	67.55	155.7	−18.20	3.3	This paper
68	Russia	NE Yakutia	Duvannyy Yar, 2002	OxA-13022	>53,200		Mandible	NC	NC	NC	68	156	−19.5		Barnett et al. (2009)
69	Russia	New Siberian Islands	Bolshoy Lyakhovskiy Island	OxA-18813	>52,600		Femur	NC	NC	NC	73.33	141.44	−19.51	3.1	This paper
70	Russia	NE Yakutia	Khromskaya Guba, Khaptashinskiy, 1978	OxA-13023	>50,600		Femur	NC	NC	NC	71.833	145.883	−20.2		Barnett et al. (2009)
71	Russia	NE Yakutia	Alazeya River, 1950s	OxA-13474	58,200	3500	Calcaneum (repeat?)	64,541	54,701	60,535	70.85	153.7	−19.05		Barnett et al. (2009)
72	Russia	NE Yakutia	Chukochya, Loc. N 27, Kolyma, 1969	OxA-13025	55,700	3000	calcaneum	60,418	52,747.5	57,262	68	156	−19.45		Barnett et al. (2009)
73	Russia	NE Yakutia	Chukochya, Loc. N 27, repeat?	OxA-13475	54,600	1700	Calcaneum (repeat?)	NC	54,335	55,972	68	156	−19.45		Barnett et al. (2009)
74	Russia	NE Yakutia	Alazeya River, 1950s	OxA-13021	55,300	2500	Calcaneum	NC	50,465	55,881	70.85	153.7	−19.05		Barnett et al. (2009)
75	Russia	Magadan, north Khabarovsk	Krestovka R., Loc. 6, 1979	OxA-13830	54,100	1800	Radius	NC	53,908	55,728	60.083	139.9	−20.3		Barnett et al. (2009)
76	Russia	New Siberian Islands	Bolshoy Lyakhovskiy Island	OxA-18812	52,000	1500	Tibia	NC	47,977	54,373	73.33	141.44	−19.17	3.1	This paper

(continued on next page)

Table 1 (*continued*)

	Country	Region	Site	Lab code	^{14}C date	Error	Material dated	Cal plus	Cal minus	Cal median	latDD	longDD	Delta ^{13}C	CN	Source
77	Russia	New Siberian Islands	Bolshoy Lyakhovskiy Island	OxA-17035	47,700	800	Mandible	52,142.5	46,115.5	48,970	73.33	141.44	−19.91	3.3	This paper
78	Russia	NE Yakutia	Duvannyy Yar	OxA-13024	46,200	1500	Calcaneum	52,861	43,894	47,780	68	156	−17.9		Barnett et al. (2009)
79	Russia	Chukotka	Kyttyk Peninsula	OxA-19359	36,550	290	Canine	41,345	40,375	41,025	69.6	167.73	−19.07	3.2	This paper
80	Russia	NE Yakutia	Duvannyy Yar, 1984	OxA-12981	28,720	160	Radius	33,349	31,998	32,717	68	156	−19.0		Barnett et al. (2009)
81	Russia	Lena Delta	Bykovskiy Peninsula	OxA-17037	28,550	140	Mandible	32,916	31,274.5	32,438	71.81	129.35	−19.03	3.1	This paper
82	Russia	Lena Delta	Bykovskiy Peninsula	OxA-17038	28,450	140	Canine	32,827.5	31,190	32,141	71.81	129.35	−19.02	3.1	This paper
83	Russia	NE Yakutia	Beryozovka River, 1970	OxA-13831	27,950	140	Ulna	32,222	30,390	31,277	68	156	−18.2		Barnett et al. (2009)
84	Russia	Indigirka	Keremsit River, Indigirka	OxA-16983	27,720	140	Mandible	31,863	30,320	30,880	70.56	149.71	−19.14	3.1	This paper
85	Russia	NE Yakutia	Yana RHS Site	Beta 173066	26,050	240	Bone	30,158	29,333	29,744	70.717	135.08			Pitulko et al. (2004)
86	Russia	Indigirka	Khroma River	OxA-17040	19,755	80	Humerus	23,203.5	22,799.5	23,006	70.7	143.04	−18.57	3.1	This paper
87	Russia	Indigirka	Khroma River	OxA-17041	19,725	75	Humerus (repeat)	23,195	22,790	22,963	70.7	143.04	−18.80	3.1	This paper
88	Russia	NE Yakutia	Alazeya River, 1972	OxA-13835	13,770	55	Radius	17,053	17,000.5	17,031	70.85	153.7	−18.80		Barnett et al. (2009)
89	Russia	Magadan	Arga-Yurekh River, 1982	OxA-13833	12,525	50	Ulna	14,962	14,628.5	14,797	62.2	146.783	−18.4		Barnett et al. (2009)
90	Russia	Lena Delta	Lena River STP	OxA-12901	12,450	60	Femur	14,918.5	14,205	14,640	72	127	−18.9		Barnett et al. (2009)
91	USA	Alaska	Cripple Creek Sump 1950	OxA-10085	53,900	2300	Ulna	NC	53,654.5	55,581	64.813	−164.501	−17.9		Barnett et al. (2009)
92	Canada	Yukon	Porcupine River	CAMS-18421 (Beta-79858)	39,300	1000	Left mandible	43,628	41,335	42,237	67.57	−136.42			Harington (2003)
93	Canada	Yukon	Thistle Creek	TO-7743	32,750	370	Mandible	39,138	35,949	37,170	63.0	−139.28			Storer (2003)
94	USA	Alaska	Fairbanks area	CAMS131360	20,970	180	Left ulna	24,930	23,606	24,356	65.04	−147.113	−18.6		Fox-Dobbs et al. (2008)
95	USA	Alaska	Fairbanks area	CAMS131361	18,590	130	Left ulna	22,681.5	21,385	21,885	65.04	−147.113	−19.6		Fox-Dobbs et al. (2008)
96	USA	Alaska	Fairbanks area	CAMS131349	18,270	130	Metatarsal II	21,999	20,464.5	21,558	65.04	−147.113	−19.6		Fox-Dobbs et al. (2008)
97	USA	Alaska	Gold Hill 1952	OxA-10084	18,240	90	Mandible	21,855	20,520	21,533	64.85	−147.92	−18.3		Barnett et al. (2009)
98	USA	Alaska	Fairbanks Creek, 1951	OxA-13452	17,890	100	Ulna	21,245	20,191	20,977	65.04	−147.113	−17.9		Barnett et al. (2009)
99	USA	Alaska	Fairbanks area	CAMS131362	17,140	110	Right tibia	20,855	19,954.5	20,076	65.04	−147.113	−19.0		Fox-Dobbs et al. (2008)
100	USA	Alaska	Fairbanks area	CAMS131346	16,650	110	Radius	19,979	19,309.5	19,724	65.04	−147.113	−18.5		Fox-Dobbs et al. (2008)
101	USA	Alaska	Fairbanks Creek, 1954	OxA-13834	16,005	65	Ulna	19,252	18,866	18,949	65.04	−147.113	−17.9		Barnett et al. (2009)
102	USA	Alaska	Banner Creek, 1938	OxA-13832	15,975	65	Mandible	19,251	18,851.5	18,945	65.518	−167.629	−18.0		Barnett et al. (2009)
103	Canada	Yukon	Hunker Creek, Dawson, 1978	OxA-10086	15,550	90	R femur	19,202	17,990.5	18,596	64.677	−165.173	−18.1		Barnett et al. (2009)
104	USA	Alaska	Fairbanks area	CAMS131347	14,050	80	Phalanx	17,502.5	17,045.5	17,318	65.04	−147.113	−19.0		12
105	USA	Alaska	Fairbanks area	CAMS131348	13,040	70	Metacarpal II	16,511	15,204.5	15,689	65.04	−147.113	−18.8		Fox-Dobbs et al. (2008)
106	USA	Alaska	Fairbanks area	CAMS131350	12,990	70	Metatarsal IV	16,503.5	15,193.5	15,649	65.04	−147.113	−18.8		Fox-Dobbs et al. (2008)

107	Canada	Yukon	Gold Run Creek	OxA-10083	12,640	75	L humerus	16,110.5	14,648	15,016	62.128	−141.906	−17.6		Barnett et al. (2009)
108	USA	Alaska	North Slope	OxA-13473	12,630	60	Bone	15,150	14,644	15,002	69	−152	−18.5		Barnett et al. (2009)
109	USA	Alaska	Lower Gold Stream, 1939	OxA-10081	12,540	75	Humerus	15,001.5	14,596	14,812	65	−147	−18.3		Barnett et al. (2009)
110	USA	Alaska	Ester Creek, 1938	OxA-13451	12,090	80	Tibia	13,976	13,635.5	13,822	64.84	−147.955	−18.6		Barnett et al. (2009)
111	USA	Alaska	Fairbanks Creek, 1955	OxA-10080	11,925	70	Humerus	13,643.5	13,094.5	13,290	65.04	−147.113	−17.8		Barnett et al. (2009)
Panthera leo															
112	Greece		Aigeira, acropolis	OxA-17155	3791	28	Pelvic fragment	4763	4531	4646	37.13	22.12	−20.34	3.3	This paper
Panthera atrox															
113	Canada	Alberta	Consolidated Pit 48, Edmonton, Alberta	OxA-13453	28,940	240	R mandible	34,432	31,244	33,220	53.64	−113.28	−17.8		Barnett et al. (2009)
114	USA	Wyoming	Natural Trap Cave, Wyoming	OxA-10078	24,080	170	Humerus	29,039	27,262	27,909	44.9928	−108.198	−17.4		Barnett et al. (2009)
115	Canada	Alberta	Consolidated Pit 48, Edmonton, Alberta	OxA-12900	11,355[b]	55	L metatarsal II	12,932	12,831	12,877	53.64	−113.28	−18.9		Barnett et al. (2009)

Key: cal median, median date calibrated using Oxcal v. 4.1. (Cariaco04); cal plus/minus: cal median ± 95.4% confidence limits; DD, decimal degrees; CN, carbon/nitrogen ratio.

OxA dates are calibrated with Oxcal (Cariaco04).

NC, not calibrated as out of range.

[a] This ultrafiltered date is from the same specimen previously dated at 27,400 ± 700 (OxA-1806) (Stuart, 1991).

[b] A lion metatarsal from Jaguar Cave, Idaho, dated at 11,900 ± 130 (OxA-919) (Gowlett et al., 1987) should be re-dated in view of recent advances in dating techniques.

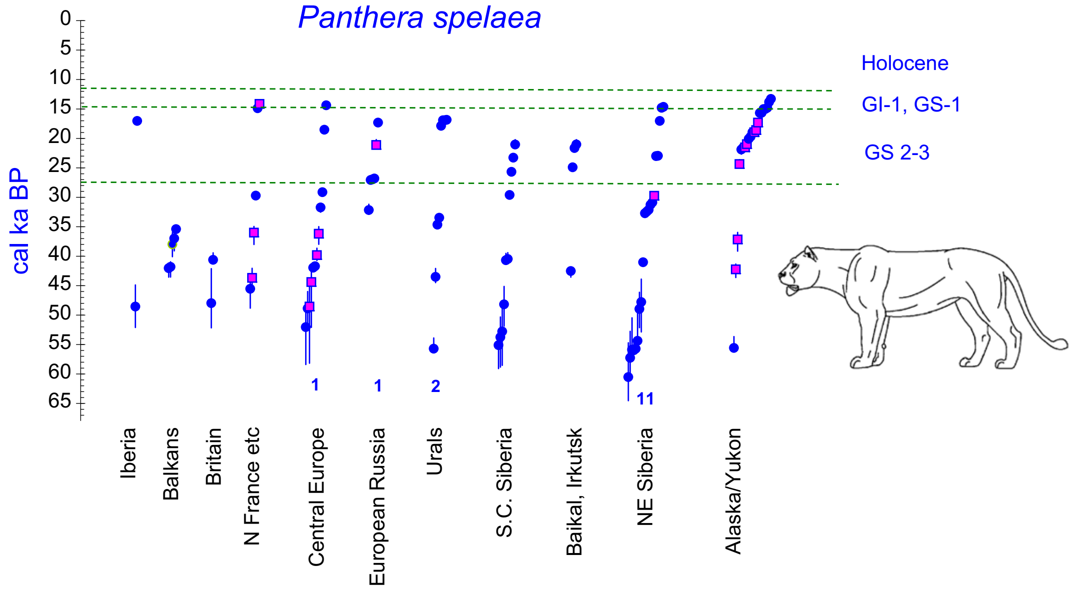

Fig. 2. Plot of calibrated AMS dates for cave lion *Panthera spelaea* arranged geographically. Oxford dates are shown blue, other labs. purple (for sources see Table 1). Median dates shown with 95.4% confidence limits. 'Northern France, etc.' includes Belgium and Netherlands; 'Central Europe' includes Austria, Germany and Poland. Numbers below series of points indicate infinite ('greater than') dates.

musk ox and reindeer, was present in this region (Macphee et al., 2002). From DNA data, there is little evidence of genetic subdivision within *P. spelaea* across Europe, Asia, and Alaska/Yukon, suggesting genetic interchange across an immense geographical range (Barnett et al., 2009).

Given that the two species do not exhibit major differences in morphology, it is likely that the cave lion had a generally similar mode of life to modern lion. However, the numerous depictions in Palaeolithic art (see below), such as the cave paintings of Lascaux, Les Trois Frères, Les Combarelles and Chauvet, France, and the small portable sculptures from La Vache Cave (France), Vogelherd Cave (Germany) and Dolni Vestonice (Czech Republic) (Bahn and Vertut, 1997; Guthrie, 2005) indicate that male cave lions lacked manes or possibly in a few cases possessed only small manes, contrasting markedly with the large and impressive manes seen in modern African and Asiatic lions. This is especially significant since these records all date from the Last Cold Stage (Weichselian, Wisconsinan), whereas in modern lions climatic influences tend to produce the opposite effect – heavier manes in cooler habitats (Kays and Patterson, 2002; West and Packer, 2002). Guthrie (1990) suggests that pride numbers might have been smaller in the cave lion, as today a prominent mane appears to be favoured when a male has to compete for the attention of a large number of females. However, this interpretation is disputed by Yamaguchi et al. (2004).

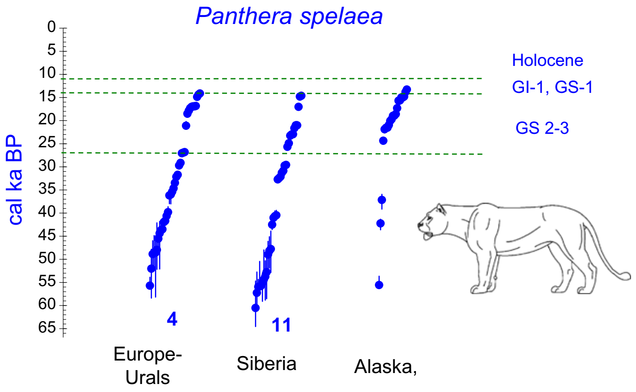

Fig. 3. Plot of calibrated AMS dates for cave lion *Panthera spelaea* (data from Fig. 2 and Table 1) combined into three geographical realms: Europe + Urals, Siberia and Alaska/Yukon. Note breaks in data ca. 25–20 ka (Europe + Urals) and ca. 40–35 ka (Siberia).

Modern African lions occupy a wide range of essentially open habitats from semi-desert to savannahs, avoiding dense forest (Haltenorth and Diller, 1980). In India lions occur in the generally rather open, dry deciduous forest of the Gir Wildlife Sanctuary. African lions are active predators, taking zebra, wildebeest, gazelles, various antelope, African buffalo and other large mammals, but also scavenging the kills of other predators, especially spotted hyaena *Crocuta crocuta*, and when necessary subsisting on smaller animals (Haltenorth and Diller, 1980). In the Gir Forest the principal prey animals include chital, nilgai, sambar, wild boar and domestic cattle. In keeping with their more forested habitat, and in contrast to lions of the African savannahs, the lions in the Gir Sanctuary hunt singly or in small groups, and tend to use ambush tactics (IUCN Red List, 2009; Mitra, 2005). Although the cave lion was probably a predominantly open-habitat predator it may also have occurred in more open woodland.

On average, cave lions were rather larger than modern lions, but sexual dimorphism in size (males are larger) is evident in both (Turner, 1984). The superbly-preserved felid trackway discovered in fine-grained fluvial deposits attributed to the mid-Weichselian, 42–35 cal ka BP, at Bottrop (Nordrhein-Westfalen, Germany), has been attributed to cave lion *Panthera spelaea* because of the very large dimensions of the paw prints (length 12–14 cm, width 12.5–15 cm) (Koenigswald and Walders, 1995; Koenigswald, 2002, p. 115). By comparison, the footprints of a modern large African male lion may measure up to 11 cm long and 12 cm across (Rosevear, 1974, p. 485). Tracks of reindeer (*Rangifer tarandus*), wolf (*Canis lupus*) and a large bovid (*Bos* or *Bison*) record part of the contemporary Bottrop fauna.

The larger size of the cave lion suggests that it could have tackled larger prey more frequently than does modern lion. In northern Eurasia the principal prey species would probably have included horse *Equus ferus*, reindeer, *R. tarandus*, giant deer

Megaloceros giganteus, red deer *Cervus elaphus*, musk ox *Ovibos moschatus*, extinct bison *Bison priscus*, and occasionally young woolly rhino *Coelodonta antiquitatis* and young mammoth *Mammuthus primigenius*. With the exception of giant deer and woolly rhino these animals also occurred in North America. Evidence that cave lions were capable of killing large and formidable prey is provided by the find of a frozen carcass of *B. priscus* (known as 'Blue Babe') from Alaska which preserves pairs of widely spaced puncture marks in the hide which match the spacing of lion canines but not those of any other contemporary carnivore, and a fragment of lion carnassial found embedded in the hide (Guthrie, 1990). The bison carcass evidently froze when only partially consumed, suggesting that only a couple of lions were involved as a large pride would have been able to eat the entire carcass before it was rendered inaccessible. On the basis of C and N stable isotope values, Matheus et al. (2003) considered *Bison* a principal food of cave lions in Beringia.

In the Late Pleistocene, carnivorous competitors of the cave lion are likely to have included spotted hyaena *Crocuta crocuta*, wolf *Canis lupus* and brown bear *Ursus arctos*. Where cave lion and hyaena ranges overlapped they very probably fought over kills as occurs in Africa today. No doubt cave lions would also have encountered and come into conflict with humans, but there is little direct evidence of this beyond their prominence in Palaeolithic art. There are a number of depictions of cave lion which can be attributed to the Aurignacian, e.g. the beautifully carved head from Vogelherd Cave, S. Germany (e.g. Koenigswald, 2002, p. 114) and the enigmatic lion-headed human figure carved out of mammoth tusk from Hohlenstein Stadel, S. Germany (Bahn and Vertut, 1997; Lister and Bahn, 2007, p. 135). Artworks attributed to the Magdalenian include cave paintings from Lascaux, Les Trois Frères and Les Combarelles, engraved stone slabs from La Marche, and the small portable sculptures from La Vache Cave – all in France (Bahn and Vertut, 1997; Guthrie, 2005), and the engravings from Gönnersdorf, Germany (see below). The age of the superb paintings, including multiple images of lion, from Chauvet Cave S.W. France is controversial (Balter, 2008; Chauvet et al., 1995). The widely–cited dating to the Aurignacian is disputed by Pettit et al. (2009) who attribute the works to the Gravettian or Magdalenian. Perforated lion canines, probably used as pendants or on necklaces are recorded from Aurignacian sites in SW France (Vanhaeren and d'Errico, 2006).

3. Results

Our dataset comprises 111 dates which have been made directly on cave lion material from northern Eurasia and Alaska/Yukon, of which 93 are Oxford AMS radiocarbon dates and 18 are AMS dates from other laboratories (Table 1). In our analyses we have only included dates where the skeletal element is specified. The Oxford dates mostly originate from our megafaunal extinctions projects but also include 20 dates produced for work on aDNA by Barnett et al. (2009). Nineteen of the dates are minimum ages ('greater than' dates). The calibrated dates (OxCal 4.1 program) are plotted in geographical groupings (Fig. 2). The table also includes three Oxford dates on *Panthera atrox* material from the USA and Canada (Barnett et al., 2009).

The plot (Fig. 2) demonstrates unequivocally that cave lion survived into the Lateglacial across much of its range. In Eurasia, the youngest dated lions are a canine from Zigeunerfels, Sigmaringen, Germany dated at 12,375 ± 50 ^{14}C BP, 14378 cal BP (OxA-17268), and the skeleton of a cave lion from Le Closeau, northern France, with a date of 12,248 ± 66 ^{14}C BP, 14,141 cal BP (AA-41882) on a metacarpal. The Le Closeau skeleton is from a stratified excavation and the date is consistent with four other dates from the context (locus 46) (Bemilli, 2000; Bodu and Mevel, 2008), although an attempted confirmatory date at Oxford on a pelvis fragment failed due to insufficient collagen. A mandible from Lathum in the Netherlands, with a widely reported date of 10,670 ± 160 ^{14}C BP (OxA-729) has recently been re-dated to 44,850 ± 650 ^{14}C BP, 45,533 cal BP (OxA-16715) (Stuart and Lister, 2007). Upper Palaeolithic engravings on slate from Gönnersdorf in the mid-Rhine region depict lions and other animals, including mammoth, woolly rhino, horse and saiga (Bosinski, 2008). These occur in very well-constrained stratified context with associated dates between ca. 14 and 16 cal ka (Stevens et al., 2009). At Riparo Tagliente, Italy, a limestone slab with a low-relief carving of a lion was found overlying a human burial (Bartolemei et al., 1974). We submitted a sample of human bone from the burial which gave a date of 13,190 ± 90 ^{14}C BP, 16,167 cal BP (OxA-10672), suggesting the presence of lion in Northern Italy post-LGM. However, the possibility that the engraving is significantly older and that the slab was re-used cannot be entirely ruled out.

The latest dates from NE Siberia are 12,450 ± 60 ^{14}C BP, 14,640 cal BP (OxA-12901) from the Lena Delta, and 12,525 ± 50 ^{14}C BP, 14,797 cal BP (OxA-13833) from the Arga-Yurekh River, Magadan. This pattern of data suggests that cave lion disappeared more or less synchronously across northern Eurasia, as the three youngest dates for Western Europe fall between 14.1 and 14.9 cal ka and the youngest two dates for north-eastern Siberia between 14.6 and 14.8 cal ka BP (Table 1, Fig. 2). However, given the limitations of the data it is possible that later survivals may yet be discovered in some areas.

The two youngest direct dates for eastern Beringia of ca. 13.3 and 13.8 cal ka BP suggest that cave lions survived for approximately a thousand years later in north-western North America than in Eurasia. The latest available date of 11,925 ± 70 ^{14}C BP (13,290 cal BP), from Fairbanks Creek, Alaska, is 1500 years older than the widely reported Lost Chicken Creek date of 10,370 ± 160 ^{14}C BP (Kurtén and Anderson, 1980; Stuart, 1991) which, however, is invalid as it was made not directly on a lion, but on a bison bone found at the same site (Barnett et al., 2009).

The data also suggest some patterning of occurrence preceding the lateglacial. Combining calibrated dates from Siberia (Fig. 3) indicates a lack of dates for the interval ca. 40–35 cal ka BP, while for Europe and the Urals, there is a reduction in the interval ca. 25–20 cal ka BP. These hiatuses can also be seen in Fig. 2, where the apparent temporal gap for Western Europe extends between about 18.5 and 29 cal ka BP. These findings must be taken with caution because of the small sample sizes, but their potential significance is discussed below.

Only three direct dates are currently available for *P. atrox* (Table 1), but the latest, 11,355 ± 55 ^{14}C BP, 12,877 cal BP (OxA-12900), from Consolidated Pit 48, Edmonton, Alberta, Canada (Barnett et al., 2009), indicates survival into late LGI-1, and is ca. 400 years younger than the latest record of *P. spelaea* from Alaska.

4. Discussion and conclusions

What caused the extinction of the cave lion? Four hypotheses can be considered: (1) the predator disappeared because of extinction of its prey species – the 'keystone hypothesis' of Owen Smith (1989); (2) prey numbers and/or their geographical ranges were drastically reduced at the time (even if they subsequently recovered); (3) the widespread reduction in open habitats, and spread of shrubs and trees; (4) human impact.

The history of likely prey species is clearly of significance in exploring this issue. Of extinct herbivores, woolly mammoth *M. primigenius*, woolly rhinoceros *Coelodonta antiquitatus* and giant deer *M. giganteus* survived into the Lateglacial across substantial parts of their range, like cave lion but in contrast to other large predators, cave bear and spotted hyaena, which disappeared much earlier (Stuart and Lister, 2007; Pacher and Stuart, 2009).

Cave lion seems to have become extinct across northern Eurasia within a few hundred years of the onset of the first part of the Lateglacial Interstadial (Greenland Interstadial GI-1e, or Bølling) which occurred at ca. 14.7 cal ka BP. The latest dates for woolly rhinoceros *C. antiquitatis* indicate that it went extinct a few hundred years earlier than cave lion across the western half of northern Eurasia, but conversely survived several hundred years later than lion in north-east Siberia (Stuart and Lister, 2007). It was absent from North America. It seems probable that the disappearance of both species had a common cause, directly or indirectly in response to the climatic warming that occurred at this time, with the associated spread of shrubs and trees and reduction in open habitats in many areas (Huntley, 1990; Litt et al., 2003). Woolly mammoth *M. primigenius* also underwent a drastic reduction in geographical range within the LGI, at ca. 13.6 cal ka BP, soon after the beginning of the Allerød (Greenland Interstadial GI-1a–c) (Stuart et al., 2002; Stuart and Lister, 2007). In the case of giant deer *M. giganteus*, range collapse was later still, in the Younger Dryas (Greenland Stadial GS-1), ca. 12.9 cal ka BP (Stuart et al., 2004). Both of these taxa are known to have survived in reduced ranges for several millennia longer, finally becoming extinct well into the Holocene (Stuart et al., 2004; Lister and Stuart, 2008; Vartanyan et al., 2008; Veltre et al., 2008). Others, such as horse *E. ferus*, musk ox *O. moschatus*, reindeer *R. tarandus* and red deer *C. elaphus* survive to the present day. Evidently the climatic warming and vegetational changes of the Lateglacial Interstadial had a profound effect on the history of the megafauna, but species were affected in different ways. Loss of open habitats may have been an additional factor affecting cave lion numbers, separately from any actual loss of prey, if they were behaviourally tied to hunting in open habitats. The adaptability of modern lions, which hunt in open forest in India, urges caution in this respect, but it could remain a potential contributing factor to the demise of cave lions if they were less competitive in closed environments.

In sum, there is a broad correlation of the extinction of *P. spelaea* with what is widely regarded as the collapse of the 'mammoth steppe' ecosystem, but the process was complex and on present evidence it is difficult to pinpoint the cause more precisely. However, the literal hypothesis that lions disappeared because of the extinction of putative prey species (cf. Owen Smith, 1989) can be discounted, as all except rhino (not a likely major prey item) survived for millennia later than cave lion. So far there is no strong evidence for significant human impact on cave lions, although more work is needed to determine the timing and extent of human population changes in the Lateglacial in order to test if there is any correlation with extinction. For example, the inferred rapid expansion of human populations about 15.5 cal ka, seen in France and Northern Europe (Gamble et al., 2004), might have contributed to the extinction of cave lion in Europe some 800 yrs later.

Events earlier in the chronology may also be significant in understanding the pattern of distributional change and ultimate extinction. Based on the study of ancient DNA, Barnett et al. (2009) demonstrated a dramatic and widespread decline in genetic diversity within *P. spelaea* across western Beringia and Europe, some time in the interval ca. 48–32 ^{14}C ka, followed by a rapid population expansion thereafter. The decline in diversity could reflect genetic drift combined with the relatively sparse sampling. However, the authors consider a geographically-widespread genetic bottleneck more likely, followed by a subsequent re-invasion and/or range expansion. The cause for the putative bottleneck is unclear, but it forms part of a growing body of evidence of major alterations in genetic structure in megafaunal populations during MIS 3 (e.g. Barnes et al., 2007), well before several of the species went extinct. The cave lion radiocarbon dataset considered by Barnett et al. (2009) was limited to specimens yielding DNA, and did not include any specimens from Asia outside Beringia. From the full dataset (Figs. 2 and 3), it appears possible that the gap in dates in the interval 40–35 ka corresponds to the bottleneck event, although this must remain provisional until a larger dataset is obtained. It also broadly corresponds to the arrival of modern people in Europe (Conard and Bolus, 2003).

The second apparent temporal gap is for Western and Central Europe between about 18.5 and 29 cal ka BP, corresponding broadly to the 'Last Glacial Maximum' (LGM) (Figs. 2 and 3). A similar gap is seen in a range of directly-dated megafaunal taxa (e.g. *M. primigenius* and *M. giganteus*: Stuart et al., 2004), although taxa vary in the timing and duration of the gap. In addition, the extinction of the cave bear *Ursus spelaeus* appears to have occurred around this time, as there are no convincing dates after ca. 27.8 cal ka BP, close to the start of Greenland Stadial 3 at ca. 27.5 cal ka BP (Pacher and Stuart, 2009). Based on associated dates collated by Sommer and Nadachowski (2006), a range of extant mammalian taxa vacated north-west and central Europe during the LGM but may have survived further to the south and east. If further data confirm that the gap in cave lion dates is real, this would indicate that the species withdrew from much of Europe for roughly nine thousand years during the 'LGM', but survived through this period in Siberia, and then re-colonized much of its former western range after about 18.5 cal ka BP. Moreover, some areas were probably not re-colonized. For example in Britain there is no record of cave lion from any Lateglacial site (Yalden, 2007) indicating that, along with other species including hyaena *C. crocuta* and bison *B. bison*, lion did not return after the 'LGM'; the only two available British radiocarbon dates on lion are both older than 40 cal ka (Table 1, Fig. 2).

The earlier history of *P. leo* outside Africa, and its relation to *P. spelaea*, are unclear. The oldest European lion fossils are of early Middle Pleistocene age, among the earliest being the specimens from the type Cromerian of West Runton, Norfolk, ca. 700 ka (Lewis et al., in press). These have been named *Panthera fossilis* or *P. leo fossilis* (REICHENAU 1906). This population presumably had its roots in Africa, and in turn was plausibly ancestral to later *P. spelaea* and *P. atrox*. Based on DNA sequence data, Burger et al. (2004) and Barnett et al. (2006) showed that modern sub-Saharan African lions are phylogenetically basal among living populations, the dispersal into North Africa–Asia being more recent. The North African and Asian animals form a distinct clade, craniologically distinguishable from sub-Saharan lions (Hemmer, 1974). However, European Pleistocene cave lions are genetically closest to sub-Saharan *P. leo* clades, not to the 'northern' *P. leo* from N. Africa and India (Barnett et al., 2006). European *P. spelaea*, and North African/Indian *P. leo*, are therefore not closely related, despite being geographically closer. While the last common ancestor of all modern lions was relatively recent at ca. 70–200 thousand years ago (Burger et al., 2004), the European *P. spelaea* lineage apparently had a more ancient derivation.

Consistent with these results, Burger et al. (2004) and Barnett et al. (2009) found no evidence for genetic interchange between cave lions and modern lions, suggesting genetic isolation of the European lineage since its origin ca. 700 ka BP. This raises the interesting question of the geographical relationship of the two species in the Late Pleistocene, a problem that is only likely to be solved by further extensive aDNA work and radiocarbon dating. Barnett et al. (2009) suggested a 'long-term contact zone in the Near East', but only a single ancient *P. leo* individual beyond Africa yielded DNA, a (presumably historical) specimen from Iran, which fell within the northern *leo* clade.

Kahlke's map (Kahlke, 1994) of the overall (time-averaged) distribution of cave lion in the Late Pleistocene indicates a southern limit in the far south of Iberia and Italy, the Caucasus, eastern Turkey, southern Siberia and Manchuria. Curiously it appears to have been absent from the Balkan Peninsula. Modern lions, on the other hand, were present in south-eastern Europe for several thousand years during the Holocene. Lion remains are recorded from a number of archaeological sites in Greece and Bulgaria, extending to Moldova, the Ukraine and Hungary (Ninov, 1999; Sommer and Benecke, 2006; Bartosiewicz, 2009; see map in Nowell and Jackson, 1996; reproduced in Barnett et al., 2006, Fig. 1). The earliest Holocene record from south-eastern Europe is based on a single fragmentary upper canine from the Karanovo tell settlement in Bulgaria (Bartosiewicz, 2009). The archaeological context (Neolithic Phase II) indicates an age of ca. 8 cal ka BP. However, as pointed out by Bartosiewicz (2009), given the absence of any other lion material of this age from Europe, it is not possible to rule out that this single tooth could have been imported as a trophy either from North Africa or south-west Asia. Another less likely possibility is that it is actually from a cave lion and could therefore be much older than its context, but this suggestion could only be tested by a direct radiocarbon date on the specimen. There are isolated later finds from Neolithic contexts: Greek Macedonia (ca. 6.46–6.0 cal ka BP) and western Hungary (ca. 5.5 cal ka BP), and more numerous records after ca. 5.0 cal ka BP from Hungary, the Ukraine, Bulgaria and Greece (Chalcolithic, Bronze Age and Iron Age). We obtained a date of ca. 4.65 cal ka BP on a lion pelvis from the Bronze Age Mycenean site of Aigeira Acropolis, Greece (Table 1). In summary we can say that lions invaded south-eastern Europe during the Holocene, presumably via the Bosphorus from Turkey, perhaps as early as 8.0 cal ka BP and probably by ca. 6.5–6.0 cal ka BP. The survival of lions in Greece ca. 2.45–2.35 cal ka BP is attested by classical authors such as Herodotus, Xenophon and Aristotle (Ninov, 1999; Sommer and Benecke, 2006; Bartosiewicz, 2009), but they had probably disappeared from the Ponto-Mediterranean region by about 2000 years ago at the end of the Iron Age (Sommer and Benecke, 2006).

It is remarkable that lion, in the form of modern *Panthera leo*, recolonized a large area of south-eastern Europe in the Holocene, ca. 6–8 millennia after the extinction of the cave lion in Eurasia. The geographical range in the Holocene was limited to areas with open vegetation including the Ukrainian and Hungarian steppe, part of the former cave lion range, but they did not penetrate the forests of Central Europe (Sommer and Benecke, 2006). Thus, in Central to Eastern Europe and in eastern Turkey there are limited areas of overlap between the Late Pleistocene range of cave lion and the Holocene range of modern lion. However, these records are not contemporary, and we have no information on the range of *P. leo* in Asia in the Late Pleistocene, so the boundary between the species at that time is unclear.

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