



# Continuity of brown bear maternal lineages in northern England through the Last-glacial period



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## ABSTRACT

Brown bears recolonised Europe rapidly after the Last Glacial Maximum (LGM), but there has been debate about whether bear populations were confined to separate glacial refugia in southern Europe, or if there was continuous gene flow among groups. To look in more detail at recolonisation routes into the British Isles after the LGM, 16 brown bear (*Ursus arctos*) samples from Lateglacial Yorkshire were analysed for mitochondrial DNA survival. The resulting data were compared with earlier work on Late Pleistocene and Holocene bears from Ireland (Edwards et al., 2011), as well as with both modern and ancient bears from across continental Europe.

The results highlight the temporal and spatial continuity of brown bear maternal lineages through the Lateglacial period in northern England. While this region was not a refugial area in the LGM for the Irish Clade 2 brown bears, our data suggest that populations of brown bear in England did act as refugial sources for the later colonisation of Ireland, by Clade 1-i bears, during the Holocene. Our results contribute to a wider understanding of the phylogenetic relationships of brown bears through the Late Quaternary, and lend a valuable perspective on bear migration into peripheral Europe.

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## 1. Introduction

Genetic variation within extant European species often reveals geographical patterns, which can be interpreted as the 'footprint of recolonisation histories' (Hewitt, 2000) after the Last Glacial Maximum (LGM). One recurring pattern is best exemplified by the phylogeography of the brown bear (*Ursus arctos*). At the end of the LGM, brown bears recolonised Europe more quickly than any carnivorous mammal species of the Holocene fauna (Sommer and Benecke, 2005). Early analysis of mitochondrial (mt) DNA from modern bears suggested three source populations for this

migration, originating in the glacial refugia of the Iberian Peninsula (Clade 1-i), the Balkans (Clade 1-b) and the Caucasus (Clade 3) (Taberlet et al., 1998). However, a study of archaeological brown bears from mainland Europe (Valdiosera et al., 2007), rather than confirming the confinement of genetic types to different glacial refugia, provided evidence of continuous gene flow across southern Europe. In any case, all brown bear matrilineal so far sequenced from Europe, whether modern or ancient, fall into either Clade 1 or 3a (Edwards et al., 2011), with western and central Europe being exclusively Clade 1-i.

It was believed that the picture in Ireland would be similar, and that Irish bears would have Clade 1-i matrilineal. However, mitochondrial analysis of a number of ancient brown bears from Ireland, both pre- and post-LGM, found that the majority grouped with modern-day polar bears in Clade 2 (Edwards et al., 2011). The taxonomic status of the polar bear has varied through time, and it is only recently that it has been considered a close relative of the brown bear (Kitchener, 2010). The palaeontological record supports a recent divergence, with polar bears believed to have evolved from

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**Table 1**  
 Details of ancient DNA analysis undertaken on brown bear remains from the British Isles. Radiocarbon date information taken from: \*Lawson (1995) and <sup>S</sup>Woodman et al. (1997); † and § = different parts/elements of the same individual.

Lab code/GenBank accession	Site information	Code for figures	Sample number	Bone element	Uncalibrated radiocarbon date (Lab number)	95.4% 2 sigma (cal. BP)	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	CR1	CR2	Clade assignment	Reference
TL01	Star Carr, North Yorkshire, England	STAR	458	Left upper canine	9533 ± 37 bp (OxA-19182)	10,890 ± 190	-20.8	5.8	Partial	No	1-i	This study
TL02	Kinsey Cave, Giggleswick, North Yorkshire, England	KC	KYC-8	Part skull	12,535 ± 55 bp (OxA-16388)	14,645 ± 367	n/d	n/d	Yes	Yes	1-i	This study
TL03	Kinsey Cave, Giggleswick, North Yorkshire, England	KC	KYC-6	Mandible	12,315 ± 55 bp (OxA-16377)	14,324 ± 303	n/d	n/d	Partial	Yes	1-i	This study
TL04	Kinsey Cave, Giggleswick, North Yorkshire, England	KC	KYC-2	Femur	12,465 ± 65 bp (OxA-19183)	14,554 ± 366	-18.8	5.2	Partial	Yes	1-i	This study
TL05	Victoria Cave, Settle, North Yorkshire, England	VC	VC-221	Mandible	10,080 ± 55 bp (OxA-X-2270-11)	11,613 ± 222	-18.9	5.2	Partial	Yes	1-i	This study
TL06	Victoria Cave, Settle, North Yorkshire, England	VC	VC-226	Mandible	9594 ± 40 bp (OxA-18991)	10,945 ± 189	-19.0	4.7	Partial	No	1-i	This study
TL07	Victoria Cave, Settle, North Yorkshire, England	VC	VC-223	Pelvic fragment	12,520 ± 50 bp (OxA-18992)	14,626 ± 358	-18.9	7.6	Yes	Yes	1-i	This study
TL08	Victoria Cave, Settle, North Yorkshire, England	VC	VC-246	Humerus	12,250 ± 55 bp (OxA-18993)	14,158 ± 216	-19.0	5.9	Yes	Yes	1-i	This study
TL09	Victoria Cave, Settle, North Yorkshire, England	VC	VC-299	Mandible	12,125 ± 50 bp (OxA-15728)	13,971 ± 137	n/d	n/d	Yes	Yes	1-i	This study
TL10	Victoria Cave, Settle, North Yorkshire, England	VC	VC-300	Mandible	12,490 ± 50 bp (OxA-15729)	14,586 ± 352	n/d	n/d	Yes	Yes	1-i	This study
TL11	Raven Scar Cave, Ingleton, North Yorkshire, England	RSC		Mandible	9000 ± 40 bp (OxA-18994)	10,188 ± 54	-21.6	0.8	Yes	Yes	1-i	This study
TL12†	Greater Kelco Cave, Giggleswick, North Yorkshire, England	GKC		Lower canine	FAILED	n/a	n/d	n/d	No amplification		n/a	This study
TL13†	Greater Kelco Cave, Giggleswick, North Yorkshire, England	GKC		Part of a canine root	10,355 ± 55 bp (OxA-X-2270-16)	12,194 ± 202	-20.4	7.7	No amplification		n/a	This study
TL14	Sewell's Cave, Settle, North Yorkshire, England	SC	(a)	Phalange	11,690 ± 45 bp (OxA-18995)	13,546 ± 135	-19.0	5.2	Yes	Yes	1-i	This study
TL15	Sewell's Cave, Settle, North Yorkshire, England	SC	(b)	Phalange	12,230 ± 50 bp (OxA-18996)	14,089 ± 149	-18.5	6.1	Yes	Yes	1-i	This study
TL16	Conistone Dib Cave, Grassington, North Yorkshire, England	CDC		Ulna	11,655 ± 45 bp (OxA-18997)	13,515 ± 137	-19.3	6.1	Yes	Partial	1-i	This study
JF900158	Carsington Pasture Cave, Carsington, Derbyshire, England	CPC	B01	Ulna	12,143 ± 46 bp (KIA26352)	13,936 ± 146	-18.9	5.8	Yes	Yes	1-i	Edwards et al. (2011)
AY082845/81	Bear Cave, Inchnadamph, Scotland	BC	RSM1962/63	Tooth	2673 ± 54 bp (BM-724)*	2801 ± 80	n/a	n/a	Yes	Yes	1-i	Barnes et al. (2002)
JF900159	Red Cellar Cave, Co. Limerick, Ireland	RCC	B02	Tibia	10,650 ± 100 bp (OxA-3704)§	12,569 ± 174	-21.2	7.0	Yes	Yes	2	Edwards et al. (2011)
JF900160	Plunkett Cave, Kesh Corran, Co. Sligo, Ireland	PC	B03	Distal humerus	11,920 ± 85 bp (OxA-3706)§	13,683 ± 182	-17.8	6.7	Partial	Yes	2	Edwards et al. (2011)
JF900161§	Foley Cave, Co. Cork, Ireland	FC	B07	Tooth	26,340 ± 320 bp (OxA-3722)§	30,937 ± 254	-16.1	9.6	Partial	No	2	Edwards et al. (2011)
JF900162§	Foley Cave, Co. Cork, Ireland	FC	B08	Tooth	26,340 ± 320 bp (OxA-3722)§	30,937 ± 254	-21.5	9.5	Yes	Yes	2	Edwards et al. (2011)
JF900163	Castlepook Cave, Co. Cork, Ireland	CC	B09	Calcaneum	33,310 ± 770 bp (OxA-4231)§	39,055 ± 1384	-19.7	5.9	Yes	Yes	1-b	Edwards et al. (2011)
JF900164	Castlepook Cave, Co. Cork, Ireland	CC	B10	Femur	37,870 ± 1270 bp (OxA-4238)§	42,618 ± 628	-20.2	6.0	Yes	Yes	1-b	Edwards et al. (2011)

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