

Quaternary history of the European roe deer *Capreolus capreolus*

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ABSTRACT

1. The European roe deer *Capreolus capreolus* is a typical faunal element of the Holocene. It was already present in Europe at least 600 000 years ago and it has been known from both glacial and interglacial phases since then. With nearly 3000 fossil and subfossil records, it is one of the most frequent mammals in the Late Quaternary.

2. During the Middle and Late Weichselian Pleniglacial, the distribution of the roe deer was not restricted to the Mediterranean peninsulas but repeatedly reached regions of central Europe. In contrast to that, roe deer records from the Last Glacial Maximum (LGM, 21.0–14.5 ka ¹⁴C BP) are largely confined to the Mediterranean peninsulas – with the exception of south-western France and the surroundings of the Carpathians where several records attest to its occurrence during the LGM.

3. During the Greenland Interstadial 1 (12.5–10.8 ka ¹⁴C BP), the species' distribution extended further north and the roe deer appeared north of the Alps and reached regions of central Germany. This seems to be correlated with the abrupt change to more favourable environmental conditions during this period. It is very likely that the roe deer disappeared north of the Alps during the Younger Dryas cooling (10.8–10.0 ka ¹⁴C BP). The northern regions of the central European lowlands were recolonized by roe deer during the late Preboreal 9.7–9.5 ka ¹⁴C BP for the first time since the Weichselian Glacial.

4. The combined pattern of genetic data and fossil records of European roe deer suggests several regions in the Iberian peninsula, southern France, Italy and the Balkans as well as in the Carpathians and/or eastern Europe as glacial refugia. It further suggests that *C. capreolus* might have recolonized most parts of central-northern Europe out of one or more eastern European (not Balkan) and/or Carpathian refugia. This recolonization wave might have blocked immigration from the traditional Mediterranean areas.

Keywords: *Capreolus capreolus*, glacial refuge, ice age, phylogeography, recolonization

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INTRODUCTION

The European roe deer *Capreolus capreolus* is a typical faunal element of the Holocene. Its distribution comprises most of Europe except for Ireland, some Mediterranean islands,

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northern Russia and the tundra regions. In Russia, its distribution is bordered by the western range of the Siberian roe deer *Capreolus pygargus*, whose species status has been supported recently by both morphological and genetic evidence (Danilkin, 1995; Lister, Grubb & Sumner, 1998; Xiao *et al.*, 2007). In line with Haldane's rule, female hybrids of the two taxa are fertile while male hybrids are not (Danilkin, 1995). Accordingly, a hybrid zone exists in the Volgograd region (Danilkin & Hewison, 1996). The roe deer's large distribution range is probably accounted for by a high adaptability to a wide variety of habitats with a preference for a mixture of woodlands and agricultural landscapes (Lehmann & Sägesser, 1986; Stubbe, 1999). The roe deer was already present in Europe at least 600 000 years ago (Middle Pleistocene, Lister *et al.* 1998), and it has been known from both glacial and interglacial phases since then. With nearly 3000 fossil and subfossil records, the roe deer is one of the most frequent mammals in the Late Quaternary.

Roe deer phylogeography has been studied by several authors over the last decade who suggested a complex postglacial recolonization pattern from different glacial refugia (see below). The aim of the present review is to evaluate critically and compare both genetic and palaeontological/archaeozoological data for a better understanding of the Quaternary history of this widespread ungulate.

MATERIAL AND METHODS

Starting with the databases of the project 'Holocene History of the European Vertebrate fauna' (Benecke, 1999), Pleistocene and Holocene data for European roe deer were collated (Table 1). Records from Inter-Pleniglacial [Oxygen Isotope Stage 3 (OIS-3)] archaeological sites were compared and completed using data recorded by the Stage 3 Project (Musil, 2003; Van Andel, Davies & Weninger, 2003). The overwhelming majority of records was recovered from

Table 1. Overview of the records of the European roe deer from different geological stages displayed in Figs 1–4

Climate phase	Climatic changes	Radiocarbon age (ka ¹⁴ C BP)	Sites with <i>C. capreolus</i> records [n]	Fig.
Oxygen isotope stage 3	Rapid stadial and interstadial oscillations (climatic changes from colder to warmer periods)	60.0–21.0	54	1
Last glacial maximum	Maximum cooling and maximal expansion of the glaciers, no warmer interstadials	21.0–14.5	29	2
Early Late Glacial	Onset of the last deglaciation	14.5–12.5	10	
Greenland interstadial 1	Rapid global warming (Meiendorf: GI1e)	12.5–12.0	24	3
	Reafforestation of Europe (Allerød: GI1a-c)	12.0–10.8		
Greenland stadial 1	Rapid cooling, decline of woodlands in northern central Europe (Younger Dryas)	10.8–10.0	7	
Preboreal	Rapid and constant global warming	10.0–9.5	12	4
Boreal	Thermophilic animals and plants in Europe	9.5–8.0	19	

For definition details of the periods see Sommer *et al.* (2008). The Weichselian Pleniglacial, which is mentioned in the text, comprises the time from the OIS-3 to the Early Late Glacial.

archaeological contexts. The age of roe deer remains could, with some exceptions of direct dates (e.g. Zigeunerfels), only be inferred from radiocarbon dates obtained for other materials from the layer in which they were found. The majority of Pleniglacial records of the roe deer, most important for this study, were supported in this way. In the case of 14 records, relative dating by means of the archaeological context was used for aging. In the case of roe deer records from the Last Glacial Maximum (LGM), only the Solutreen culture (21.0–16.0 ka ^{14}C BP) was used as a temporal marker for relative dating of roe deer remains. Late Glacial (Greenland Interstadial 1 and Greenland Stadial 1) and Holocene records of the roe deer were mostly radiocarbon-supported with a few cases being dated using palynological data, because the relatively highly resolved climatic chronology based on pollen stratigraphy yields reliable assignments of faunal remains to a climatic epoch of the Late Glacial and Holocene. In the case of the Abri site Zigeunerfels near Sigmaringen, southern Germany, the review of the mammalian fauna, which had so far only been preliminarily published by von Koenigswald (1972) and von Koenigswald & Taute (1974), yielded new biostratigraphic information. This, in combination with newly acquired radiocarbon dates, led to a very reliable and detailed assignment of the cultural horizons (cf. Taute, 1972). All roe deer specimens from the Zigeunerfels locality were derived from the Preboreal stratigraphic complex.

The sites of all European roe deer records with precise temporal information were plotted on maps for the different periods to give an accurate visualization of the Late Pleistocene and Holocene distribution patterns of *C. capreolus* in Europe and to provide a basis for the discussion of the dynamics of regional dispersal and disappearance of the species through time. For the early Holocene, we only included records that could be unequivocally assigned to the Preboreal or Boreal. The phylogeographical data were selected from the relevant literature. For a better understanding of the radiocarbon data, all dates younger than 12.5 ka ^{14}C BP (12.8 ka cal. BC) are additionally calibrated in calendar years BC (cal. BC). Calibration of all ^{14}C -dates was conducted with the software CalPal by Weninger *et al.* (<http://www.calpal.de>) and the calibration curve Intcal98 (Stuiver *et al.*, 1998).

SPATIOTEMPORAL PATTERN OF FOSSIL RECORDS

Pleistocene

During the middle and late Pleniglacial, the distribution of the roe deer was not restricted to the Mediterranean peninsulas. During the OIS-3 (60.0–21.0 ka ^{14}C BP), *C. capreolus* repeatedly reached regions of central Europe (Fig. 1). It is remarkable that the roe deer is present in all three investigated time slices of the OIS-3 and reached the area in western and eastern central Europe north of the Alps between 60–40, 40–30 and between 30–21 ka ^{14}C BP (Fig. 1). This is probably accounted for by favourable climatic conditions during the milder interstadials (Greenland Interstadials 18-2, for an overview see Dansgaard *et al.*, 1993), which are probably also the reason for the occurrence of other species like the red deer *Cervus elaphus* (Sommer *et al.*, 2008), the polecat *Mustela putorius* (Münzel *et al.*, 2001) or the common shrew *Sorex araneus* (Rzebik-Kowalska, 2003) during the Pleniglacial in central Europe. Recent studies have also shown that several temperate species must have occurred in southern central Europe during cold stages of the last glacial cycle that were located in areas of sheltered topography providing a suitable microclimate (Sommer & Nadachowski, 2006). In contrast to the red deer, which occurred north of the Alps and on the British Isles during the Pleniglacial (Sommer *et al.*, 2008), for roe deer there is only little evidence of a colonization of the region immediately north of the Alps (Fig. 1).

The distribution pattern of fossil roe deer records from the beginning of the LGM at 21.0 ka ^{14}C BP *sensu stricto* is clearly different from the one described for the Pleniglacial

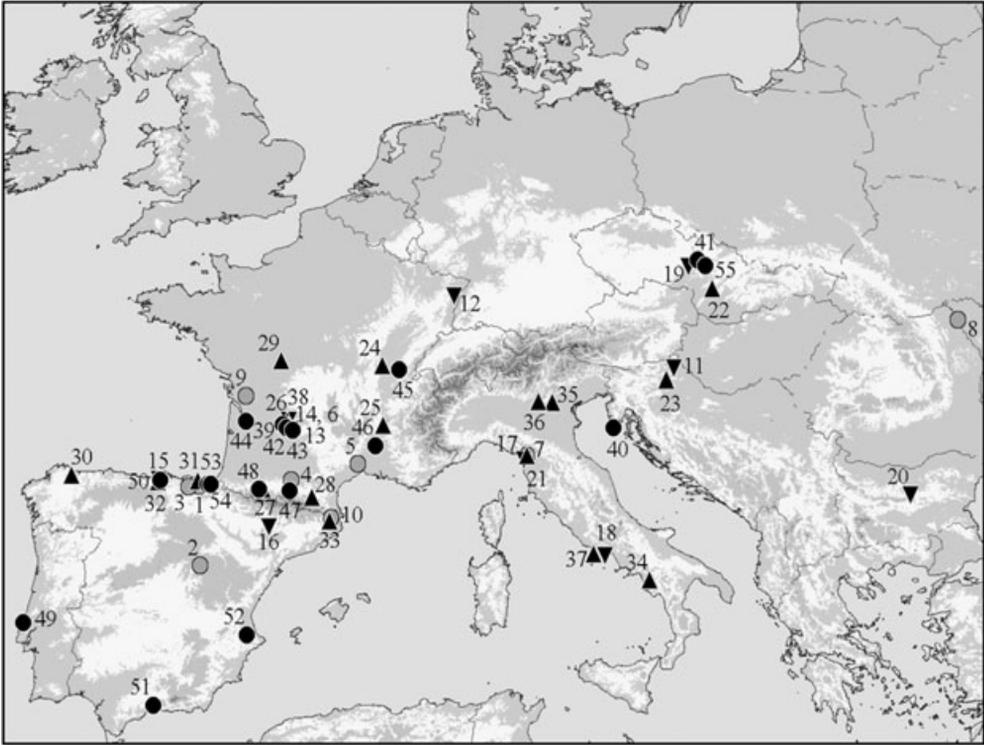


Fig. 1. Weichselian Pleniglacial (OIS-3 stage) records of the European roe deer. Reversed triangles: 60–40 ka ^{14}C BP, triangles: 40–30 ka ^{14}C BP, black circles: 30–21 ka ^{14}C BP, grey circles: 60–21 ka ^{14}C BP (no precise dating available). For scale see Fig. 6. Legend: Weichselian Pleniglacial 60–21 ka ^{14}C BP: 1 Lezetxiki, 2 Cueva de Los Casares, 3 Axlor, 4 Cueva de Isturitz y Saint-Mart, 5 Grotte de l'Hortus, 6 Combe-Grenal, 7 Buca della Iena, 8 Duruitor (Schicht 2), 9 Roche a Pierrot, 10 L'Abreda. 60–40 ka ^{14}C BP: 11 Veternica, 12 Achenheim, 13 Combe Grenal, 14 Regourdu, 15 Cueva de el Pendo, 16 Los Moros, 17 Buca della Iena, 18 Grotta di Sant'Agostino, 19 Kulna Cave, 20 Bacho Kiro. 40–30 ka BP: 21 Grotta del Capriolo, 22 Čertova Pec, 23 Krapina, 24 Velars Etrigny, 25 A. Moula (Soyons), 26 Castanet, 27 Gouffre d'Abdala, 28 Caune de Belvis, 29 Abri Rousseau, 30 Valina, 31 Cueva de Ekain, 32 Castillo, 33 Reclau Viver, 34 Castelcivita, 35 Grotta di Paina, 36 Abri Fumane, 37 Grotte Breuil. 30–21 ka ^{14}C BP: 38 Abri Pataud, 39 La Ferrassie, 40 Sandalia II, 41 Předmosti, 42 Le Flageolet, 43 Roc de Combe, 44 Roc de Marcamps, 45 Grotte de la Baume, 46 St. Marcel, 47 Grotte d'Enlene, 48 Grotte de Courau, 49 Columbeira, 50 Cueva de Morin, 51 Zafarraya Cave, 52 Cova Negra, 53 Amalda Cave, 54 Cueva de Aitzbitarte V-VI, 55 Predmosti.

(compare Figs 1 and 2). The distribution of the roe deer is now largely confined to southern Europe – with the exception of south-western France and the surroundings of the Carpathians where several records attest to its occurrence during the LGM (Fig. 2). The few records from the early Lateglacial (14.5–12.5 ka ^{14}C BP) are located within the known range of the LGM distribution of *C. capreolus* (Fig. 2). This lack of records in the northern regions over a period of nearly 10 000 years is accounted for by the unfavourable environmental conditions during the LGM in Europe (see Sommer & Nadachowski, 2006).

During the Greenland Interstadial 1 (GI1) the northern range of the roe deer distribution changed significantly: (i) it extended further north and reached the low mountain ranges of Germany; and (ii) the roe deer appeared in the region immediately north of the Alps, an area which was one of the most strongly affected landscapes during the LGM. From the GI1, there

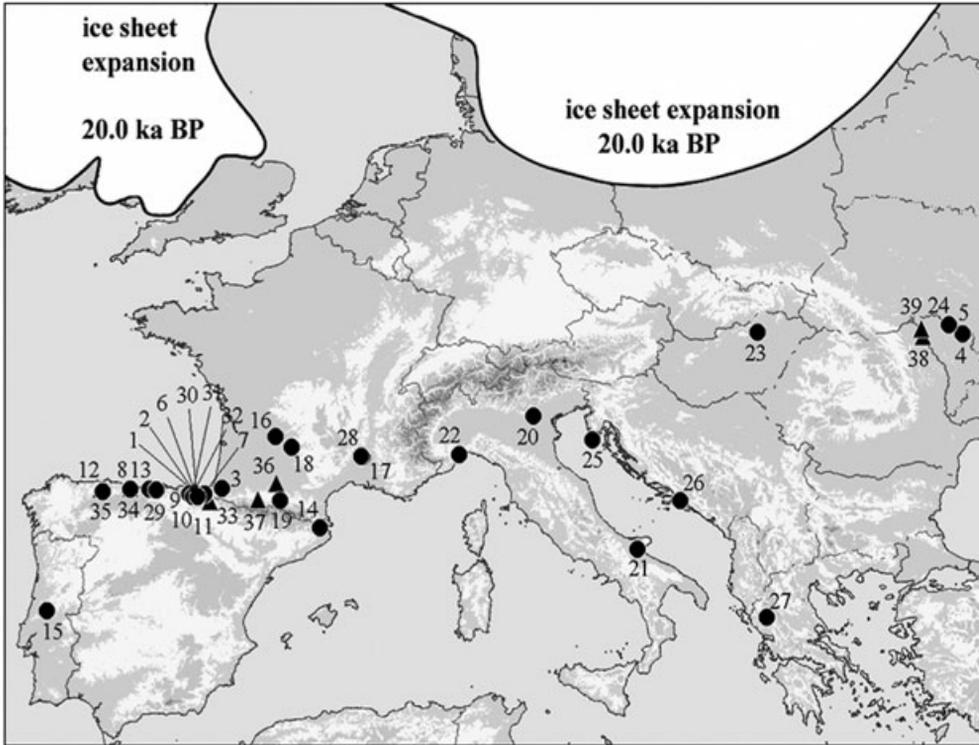


Fig. 2. Last Glacial Maximum records (21.0–14.5 ka ^{14}C BP, circles) and early Late glacial records (14.5–12.5 ka ^{14}C BP, triangles) of the European roe deer. Reconstruction of the ice sheets after Bowen *et al.* (2002) and Lundqvist & Saarnisto (1995). For Scale see Fig. 6. Legend: Last Glacial Maximum 21.0–14.5 ka ^{14}C BP: 1 Cueva de Amalda (Solutr en), 2 Cueva de Ermitia (Solutr en), 3 Cueva del Cueto de la Mina (Solutr en), 4 Rascov V (19.0–18.0 ka BP), 5 Cosauti I (17.2–17.0 ka BP), 6 Cueva de Urtiaga (17.0 kaBP), 7 Cueva de Aitzbitarte IV (18.0 ka BP), 8 Cueva de La Riera (20.9–20.4 ka BP), 9 Cueva de Santimami e (Solutr en), 10 Lezetxiki (Solutr en), 11 Cueva de Eralla (16.3–16.2 ka BP), 12 Cueto de la Mina (Solutr en), 13 Cueva de Altamira (Solutr en), 14 L'Abreda (22.6–20.1 ka BP), 15 Caldeir o (19.9–20.4 ka BP), 16 Abri Pataud (18.5–22.9 ka BP), 17 Grotte St. Marcel (20.1 ka BP), 18 Grotta Pegourie (17.5 ka BP), 19 Grotte d'Enlene (21.5 ka BP), 20 Grotta di Paina (19.4–20.1 ka BP), 21 Grotta Paglicci (19.6–20.2 ka BP), 22 Arene Candide (19.4–20.5 ka BP), 23 Balla Cave (22.3 ka BP), 24 Cosauti I (17.0–17.2 ka BP), 25 Sandalia II (21.7–22.6 ka BP), 26 Zmijinac Pecina (19.4 ka BP), 27 Kastritsa (20.8–20.2 ka BP), 28 Grotte de La Baume d'Oullins (20.1–16.1 ka BP), 29 Cueva de Morin (20.0 ka BP). Early Late Glacial 14.5–12.5 ka ^{14}C BP: 30 Cueva de Erralla, 31 Cueva de Ekain, 32 Cueva de Ermitia, 33 Cueva de Abauntz, 34 Cueva de La Riera, 35 Cueva de la Paloma, 36 Abri Dufaure, 37 Bois du Cantet, 38 Coste y I, 39 Brynzeny I.

are several records in the former periglacial areas in Germany and France (Fig. 3, No. 1, 2, 4, 5, 18, 19, 20, 21, 22). The earliest of these were dated to 12.3–12.0 ka ^{14}C BP (12.6–12.0 ka cal. BC) in Thuringia (eastern Germany) and Baden-Wurttemberg (southern Germany, Brunnacker *et al.*, 1977; Musil, 1980; Hedges *et al.*, 1998; Gietz, 2001; Benecke *et al.*, 2006; Fig. 3, No. 5, 19, 22) and belong to the so-called 'Meiendorf' interstadial (GI1e) which was characterized by an abrupt warming and reforestation with birch trees (Litt & Stebich, 1999; Litt *et al.*, 2001).

During the B lling, Older Dryas, and Aller d [GI1(a–c)], the distribution area of the roe deer expanded as far north as the Central Rhine Valley and the Thuringian Forest. There are no fossil records of the roe deer from anywhere north of the Alps that have been reliably

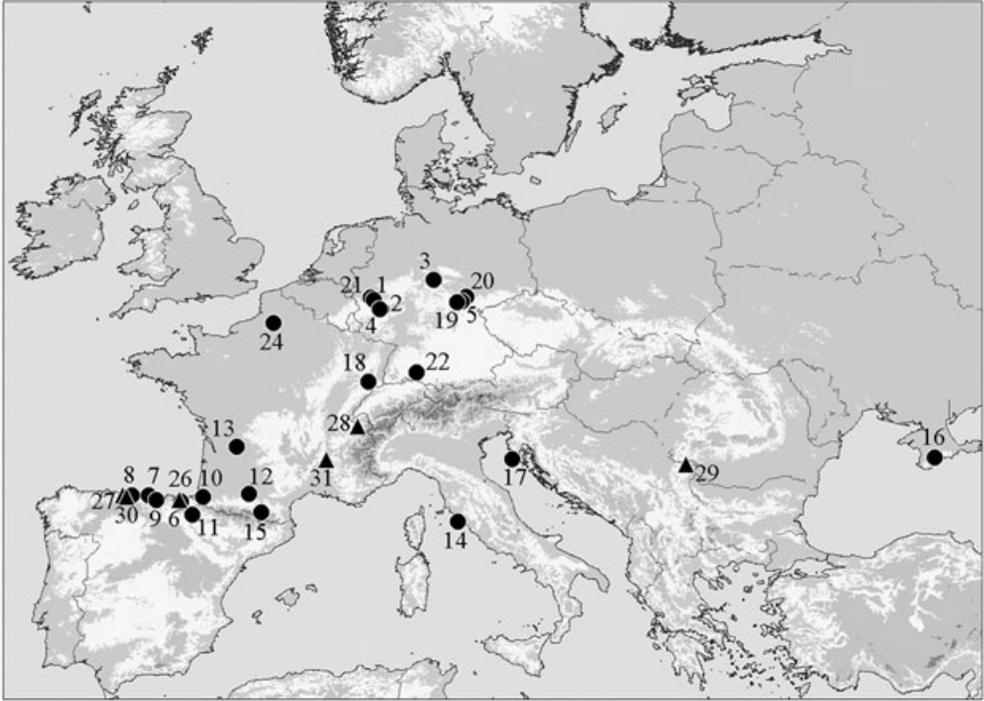


Fig. 3. Late Glacial records of the European roe deer. Circles: Greenland Interstadial 1 (12.5–10.8 ka ^{14}C BP/12.7–10.8 ka cal. BC), triangles: Greenland Stadial 1 (10.8–10.0 ka ^{14}C BP/10.8–9.6 ka cal. BC). For Scale see Fig. 6. Legend: Greenland Interstadial 1 (12.5–10.8 ka ^{14}C BP) with information (if available) on the climatical epoch GI1e = 12.5–12.0 ka ^{14}C BP ('Meiendorf'), GI1a-c = 12.0–10.8 ka ^{14}C BP (Allerød). 1 Oberkassel, 2 Kettig (GI1a-c), 3 Bettenroder Berg, 4 Miesenheim (GI1a-c), 5, Obernitz (GI1e), 6 Cueva de Erralla (GI1e), 7 Cueva de Morin, 8 Cueva del Otero, 9 Cueva del Valle, 10 Cueto de la Mina, 11 Zatoya, 12 Abri Dufaure, 13 Grotte de Rochereil, 14 Arma dello Stefanin, 15 Grotte des Eglises (GI1a-c), 16 Špan Koba (GI1a-c), 17 Sandalia II (GI1a-c), 18 Abri des Cabones, 19 Abri Fuchskirche (GI1e), 20 Oelknitz, 21 Bad Breisig (GI1a-c), 22 Burghöhle Dietfurth (GI1e) 24 Saleux (GI1a-c). Greenland Stadial 1 (10.8–10.0 ka ^{14}C BP): 26 Cueva de Urtiaga, 27 Cueva de Tito Bustillo, 28 Vieille Église/La Baume de Thury, 29 Cuina Turcului, 30 Cueva de La Riera, 31 Aven des Iboussieres.

radiocarbon-dated to the Greenland Stadial 1 (Younger Dryas, 10.8–10.0 ka ^{14}C BP, 10.8–9.5 ka cal. BC) (Fig. 3). Environmental conditions changed fundamentally in the Younger Dryas. The birch-pine forests which had grown in northern central Europe during the later GI1(a–c) disappeared and an open park tundra with only scarce tree and shrub vegetation spread out in central Europe (Usinger, 2004). The northernmost radiocarbon-supported records of roe deer are from France, west of the Alps (Fig. 3). However, the vegetation in southern Germany north of the Alps is described as light pine and birch forest (Wille, 1981; Eusterhues *et al.*, 2002). This could have been appropriate roe deer habitat, as was the case further north during the GI1 (Fig. 3).

Taking into account all available data, an absence of European roe deer north of the Alps during the Younger Dryas seems most probable; at the most, small and isolated populations may have occurred which were too small to be regularly hunted by prehistoric humans. In contrast to that, the red deer, which showed comparable reactions to the climate warming during the GI1, was present even on the British Isles during the Younger Dryas (Sommer *et al.*, 2008).

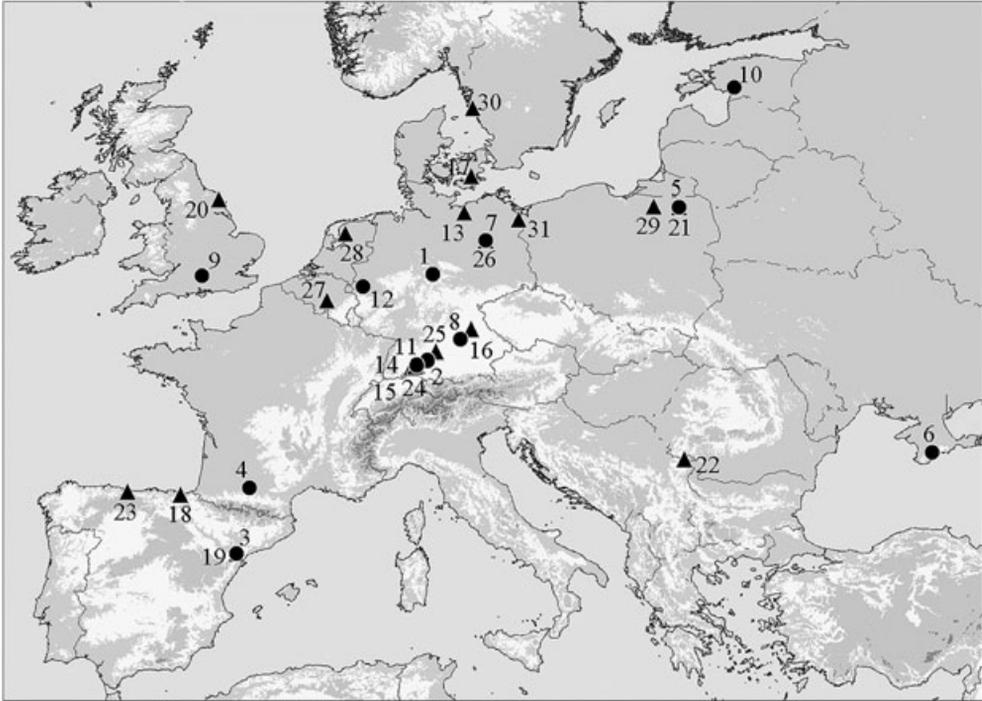


Fig. 4. Early Holocene records of the European roe deer. Circles: Preboreal (10.0–9.5 ka ^{14}C BP/9.5–8.9 cal. BC), triangles: Boreal (9.5–8.0 ka ^{14}C BP/8.9–6.9 cal. BC). For scale see Fig. 6. Legend: Preboreal (10.0–9.5 ka ^{14}C BP/9.6–8.6 cal. BC): 1 Bettenroder Berg, 2 Felsställe, 3 Grotte du Bignalats, 4 Abri Dufaure, 5 Dudka (Fst. 1), 6 Špan Koba, 7 Friesack, 8 Euerwanger Bühl bei Greding, 9 Thatcham, 10 Pulli, 11 Zigeunerfels, 12 Bedburg. Boreal (9.5–8.0 ka ^{14}C BP/8.6–7.1 cal. BC): 13 Hohen Viecheln, 14 Jägerhaushöhle, 15 Inzigkofen, 16 Bettelküche, 17 Lundby, 18 Cueva de Urtiaga, 19 Grotte du Bignalats, 20 Star Carr, 21 Dudka, 22 Cuina Turcului, 23 Cueva de La Riera, 24 Burghöhle, 25 Malerfels, 26 Friesack, 27 Namur, 28 Zutphen, 29 Tłokowo, 30 Bua Västergård, 31 Rothenklempenow.

Holocene

The early Holocene distribution of *C. capreolus* is completely different from the situation during the Younger Dryas. Roe deer remains from the Zigeunerfels directly dated to 9960 ± 50 BP (9487 ± 127 cal. BC, Poz-20317) and 9905 ± 40 BP (9359 ± 46 cal BC, KIA-26996) document the reoccupation of the area immediately north of the Alps by very early Preboreal times right at the beginning of the climatic amelioration. There are reliable radiocarbon-dated records (Lõugas, 1997; Gramsch, 2000) indicating that the northern regions of the central European lowlands were colonized by the roe deer already during the late Preboreal 9.7–9.5 ka ^{14}C BP (9.1–8.9 ka cal. BC) (Fig. 4). The directly radiocarbon-dated roe deer bone from Thatcham with a result of 9430 ± 100 BP (8813 ± 206 cal. BC, OxA-5190) also shows that southern England was inhabited by the late Preboreal (Fig. 4). During the Preboreal, the central European lowlands were slowly reafforested by birch and pine woods (Usinger, 2004). The environmental conditions for temperate and thermophilic animal species must have improved rapidly, as also demonstrated by the northward expansion of the pond turtle (Sommer *et al.*, 2007).

By Boreal and Atlantic times, when central Europe had been completely reafforested and the mean temperature was higher than today, the roe deer probably occurred in most of

central Europe (Fig. 4). The roe deer from the Mesolithic sites of Zutphen in the Netherlands dated to 9240 ± 60 BP (8440 ± 100 cal. BC, GrA-16850) and Rothenklempenow in north-eastern Germany dated to 9.3 ka BP (8.5 ka cal. BC) confirm the species' presence in the north-western part of the European lowlands in the early Boreal (Gronewoudt *et al.*, 2001; Kaiser *et al.*, 2003). The postglacial appearance of the European roe deer in Denmark and Scandinavia is discussed by Hufthammer & Aaris-Sørensen (1998) and Aaris-Sørensen (2000). From the Atlantic, there are 141 records of *C. capreolus* (not mapped). The density of the records increases with time but there is no visible further expansion. Thus, in northern regions like Finland, where the European roe deer is completely absent from Holocene subfossil sites (Ukkonen pers. comm.), the colonization must have taken place much later in the Holocene.

PHYLOGEOGRAPHY

Several phylogeographical studies on the roe deer have been carried out over the past decade. An early analysis, based on a very limited sampling of mitochondrial DNA control region sequences, yielded a western and an eastern clade, and the authors interpreted their data as being indicative of either two glacial refugia, or alternatively and more likely, a single refugium in western Europe from which Europe was subsequently recolonized (Wiehler & Tiedemann, 1998).

In a much more comprehensive study with samples from many European localities (although sample sizes were usually still small), Vernesi *et al.* (2002) again found two major mtDNA control region clusters, one eastern group (Poland, Slovakia, Bulgaria, Austria, Slovenia and Hungary) and one from the west. The latter group was divided into three subgroups, two from the Italian peninsula (Florence/Arezzo and Siena/Castelporziano, respectively) and one from Spain, France, Norway, Poland and the Alps. The introduction of eastern European roe deer to Liguria was found to have left a clear genetic signature, showing the high phylogeographic resolution of the molecular marker chosen. The conclusion drawn by the authors was the existence of three southern refugia in Iberia, Italy and the Balkans with a possible fourth refuge in Italy – the Siena/Castelporziano group, which is often regarded as a distinct roe deer taxon (*C. c. italicus*, see below). Roe deer from Italy, according to this scenario, did not spread over the Alps, and roe deer from Iberia prevail in northern Europe (Vernesi *et al.*, 2002). This would be a biogeographic history very similar to that of another European cervid species – the red deer which also seems to have recolonized large parts of Europe including the north from an Iberian glacial refuge (Ludt *et al.*, 2004; Sommer *et al.*, 2008; Skog *et al.*, in press) – and a couple of other species as well (the 'bear pattern' after Hewitt, 1999, which shows Iberian and eastern recolonization of Europe).

Randi *et al.* (2004) studied roe deer phylogeography based on mtDNA control region sequences and nuclear microsatellite loci from more than 600 European samples. They found three mtDNA clades: an eastern one comprising Serbia, Montenegro, Kosovo, Greece, the Italian Alps, the northern Apennines and Germany; a western one containing haplotypes restricted to Portugal and Spain and a subclade from the central Italian Alps; and a central one which was widespread in central and northern Europe and Italy, eastern Europe (but not Greece) and western Europe (Spain and Portugal). Clade Central also comprised a distinct subclade for the roe deer from central-southern Italy, which has been shown to be genetically distinct from other European populations and has been classified as *C. c. italicus* (see Randi, Pierpaoli & Danilkin, 1998; Lorenzini, Lovari & Masseti, 2002). Clade East probably originated in the Balkans, while Clade West is likely to have an Iberian origin. Clade Central was hypothesized by Randi *et al.* (2004) to originate either from the Balkans (because of the high

genetic diversity in Serbia, Montenegro and Kosovo) or Iberia, and the isolated *C. c. italicus* subclade is believed to represent an additional southern Italian refuge during the last glacial maximum.

The use of different molecular markers is advisable as it has often been shown that different markers do not yield concordant results (for an example in roe deer see Zachos, Hmwe & Hartl, 2006), but in this case both mtDNA sequences and microsatellites gave a similar picture: differentiation of peripheral populations (northern Iberia, southern Italy) vs. greater admixture in central Europe and the Balkans. This pattern possibly reflects both historical vicariance in southern refugia and secondary contact, or alternatively, anthropogenic impacts. Randi *et al.* (2004) found no signs of a recent European bottleneck in roe deer, but overall high haplotype diversity (0.971) and rather low nucleotide diversity (0.011) along with mismatch distribution analyses of mitochondrial haplotypes suggest the expansion of two distinct mitochondrial clades, possibly around 200 000 and 130 000 years ago which would (roughly) coincide with the penultimate and the last interglacial, respectively.

Lorenzini & Lovari (2006), in a similarly comprehensive study of mtDNA restriction fragment length polymorphisms and microsatellites, confirmed the presence of three roe deer lineages. Based on their sampling, they found an Iberian lineage, one from eastern and southern Europe (Romania, Poland, Lithuania, Italy, Turkey and Greece) and a third lineage from central and northern Europe (France, Denmark and Sweden). The Italian Alps and Austria were somewhat intermediate between the south-eastern and the central-northern lineages. There were some inconsistencies (e.g. a French haplotype in the Iberian lineage), but these may have been caused by human interferences and do not question the basic pattern. Bayesian structure analyses of the microsatellite data were concordant with mtDNA findings in that both the Iberian and the Italian peninsula showed a substantial internal substructuring (Lorenzini *et al.*, 2002, 2003; Lorenzini & Lovari, 2006). The Italian data confirmed the distinctness of the central and southern *C. c. italicus* roe deer, and the Iberian data supported a differentiation of northern vs. southern roe deer. The latter showed haplotypes not found anywhere else, which indicates long-term isolation (see also Lorenzini *et al.*, 2003). Royo *et al.* (2007), based on mtDNA control region sequences and microsatellites, confirmed the presence of two Iberian groups of roe deer, a central-southern group and a north-western group which they called Celtic-Iberian. From this, they inferred two Iberian glacial refugia, one in the north-west including the Cantabrian branch and the Galician massif and one in central-southern Iberia including the Tajo river basin and the Mediterranean coast. The genetic differences between northern and southern Iberian roe deer are also reflected by morphological differences in skull shape, which are probably adaptations to different kinds of food (Aragón *et al.*, 1998), and coat pattern (Geist, 1998).

Lorenzini & Lovari (2006) conclude that the postglacial recolonization of northern Europe was probably due to range expansion from one or more refugia in central and eastern Europe rather than from the Mediterranean areas. The Balkans with their mountain ranges extending in a north-south direction appear suitable for a postglacial northward expansion, while the refugia in Iberia and Italy remained isolated, which is in line with the high number of endemic mammals harboured by these two peninsulas (Bilton *et al.*, 1998; Frati *et al.*, 1998). It is also in accordance with the high genetic diversity in eastern roe deer, which was interpreted by Randi *et al.* (2004) as possible evidence of a recolonization of central and northern Europe from an eastern refuge, and would match the extension of broad-leaf forests from the east (Petit *et al.*, 2003). This pattern of an eastern recolonization, Hewitt's 'grass-hopper pattern' (Hewitt, 1999), however, has been questioned by Royo *et al.* (2007) who

found several haplotypes from the central clade in Iberia as well so that, according to these authors, an Iberian origin of this clade and an Iberian recolonization of central and northern Europe cannot be ruled out.

Thus, to sum up, the general picture emerging is as follows. There are three large groups of European roe deer: a western, an eastern and a central-northern one. The western and the eastern groups are by-and-large confined to Iberia and south-eastern Europe, respectively. The origin of the central-northern clade is still under debate (see below for further discussion) – Iberia, the Balkans and additional eastern refugia have been assumed as potential candidates.

Further, the data unequivocally showed significant differentiation within Iberia and Italy, suggesting two different refugia in each of the two peninsulas. As a result, in the southern parts of Iberia and Italy, there are still genetically distinct roe deer, sometimes recognized taxonomically as *C. c. garganta* in Spain and *C. c. italicus* in Italy.

ROE DEER REFUGE AREA THEORY: A SYNTHESIS OF THE FOSSIL AND MOLECULAR DATA

From the fossil record it becomes obvious that during the Weichselian Pleniglacial, the European roe deer was not completely confined to the Mediterranean peninsulas. Southern France as well as what is today the Czech Republic and Croatia were inhabited continuously or colonized repeatedly during different stages of the Pleniglacial. The genetic pattern with three distinct clades is difficult to explain by referring only to the western and eastern clades as possible source pools for central and northern Europe. If Europe was recolonized by one or both of the traditional glacial refugia (Iberia, Balkans), one would expect two distinct clades, not three. This is the case in another cervid, the red deer, where basically two distinct large clades (Iberian and Balkan) with different geographic extents have been found (see Sommer *et al.*, 2008; Skog *et al.*, in press). Even if central and northern Europe were largely admixed, harbouring roe deer descended from Iberia and the Balkans, there would still be two clades, with some central-northern roe deer clustering in the western clade and the rest in the eastern clade. The genetic pattern found, however, is different from these expectations. There are two geographically restricted clades, one in Iberia and one in the south-east. The Iberian clade also comprises some haplotypes found in the Italian Alps, which has been interpreted as evidence of either postglacial colonization of the Alps from Iberia (Randi *et al.*, 2004) or of two different glacial colonization events (Royo *et al.*, 2007). In any case, neither of these two restricted clades contributed much to the recolonization of central-northern Europe. Only two German roe deer were found to belong to the eastern clade (Randi *et al.*, 2004), which can easily be accounted for by human translocations that are known to have occurred (e.g., Niethammer, 1963) – this is hardly a ringing endorsement of a Mediterranean origin of the postglacial roe deer populations in central and northern Europe. In game species, human impacts through translocations in historical times are likely to blur the natural phylogeographic relationship and may explain single cases of non-concordance between geography and phylogeny, but they are certainly not solely responsible for the fact that there is no clear assignment of central and northern European roe deer to either the western or the eastern clade. This conclusion is supported by the fact that many roe deer translocations have failed (Niethammer, 1963). In the case of Italy, however, translocations played an important role, and accordingly, the fact that haplotypes from the Italian Alps and the Apennines have been found in central and eastern Europe has to be viewed with great caution from a phylogeographic point of view. Translocations that are known to have been carried out with central and eastern European animals after the

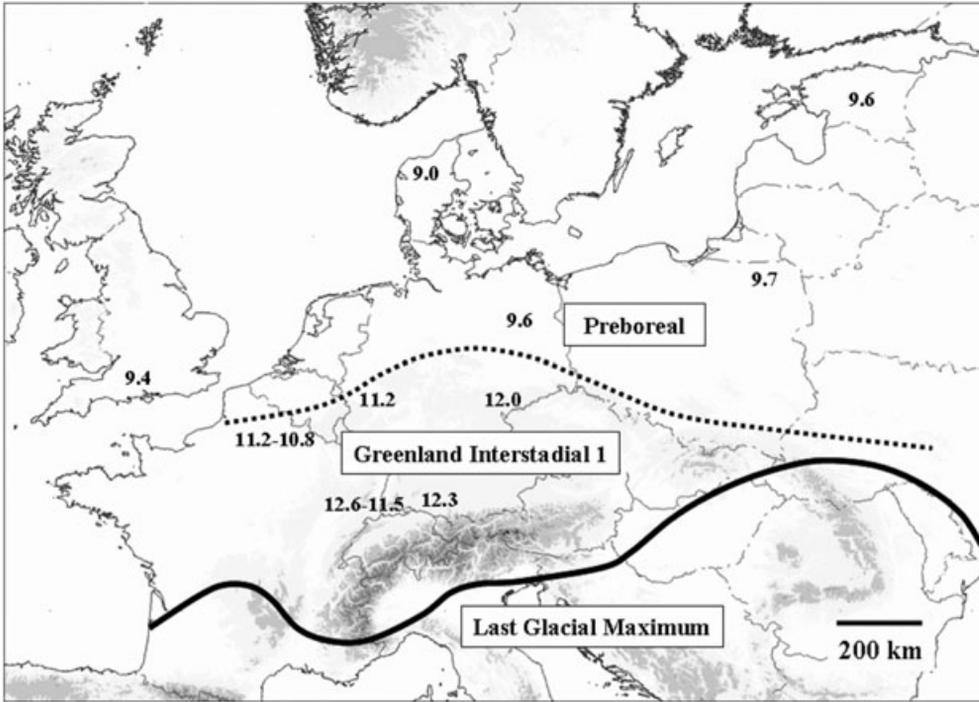


Fig. 5. Stepwise spatiotemporal recolonization model on the basis of fossil data since the LGM. The solid black horizontal line indicates the northern edge of roe deer distribution during the LGM. The black horizontal dotted line depicts the northern border of the range expansion during the Greenland Interstadial 1 (GI1) in the Late Glacial (12.5–10.8 ka ^{14}C BP). Below this line the position and time of the earliest radiocarbon-supported subfossil records of *C. capreolus* during the GI1 are displayed. Figure 3 shows the detailed position of all fossil records from this period. Above the dotted line *C. capreolus* is recorded in the early postglacial (Preboreal and Boreal) for the first time. The most important earliest radiocarbon-supported records (in ka ^{14}C BP) from this time are highlighted.

eradication of roe deer in northern Italy (with the possible exception of the eastern Italian Alps) have almost certainly blurred the natural genetic structuring and relationships (Randi *et al.*, 1998). Therefore, a recolonization of central Europe from Italy seems unlikely. The Alps were probably an effective barrier to a northward expansion, as they were for many other species (Taberlet *et al.*, 1998). In contrast to this, roe deer from the eastern Italian Alps (which are believed to harbour autochthonous roe deer) and the Balkan populations may have been connected by natural genetic exchange through low passes in the eastern Alps or along the Adriatic coast throughout much of the Pleniglacial and LGM (when the northern Adriatic sea lay dry) and not only since the early postglacial as hypothesized by Lorenzini & Lovari (2006).

The fossil record nicely reflects the climatic oscillations at the end of the last glacial. First, a sudden range expansion into the low mountain range of central Europe north of the Alps shortly after 12.5 ka ^{14}C BP (Fig. 5) was followed by an extinction in this area in the Younger Dryas (10.8–10.0 ka ^{14}C BP). Second, a range expansion took place in the course of the climatic changes at 10.0 ka ^{14}C BP/9600 cal. BC, which led to the recolonization of the central European lowlands and Scandinavia in the Preboreal and Boreal, respectively (Fig. 5). But perhaps the most important result of the analysis of the fossil record is the presence of roe

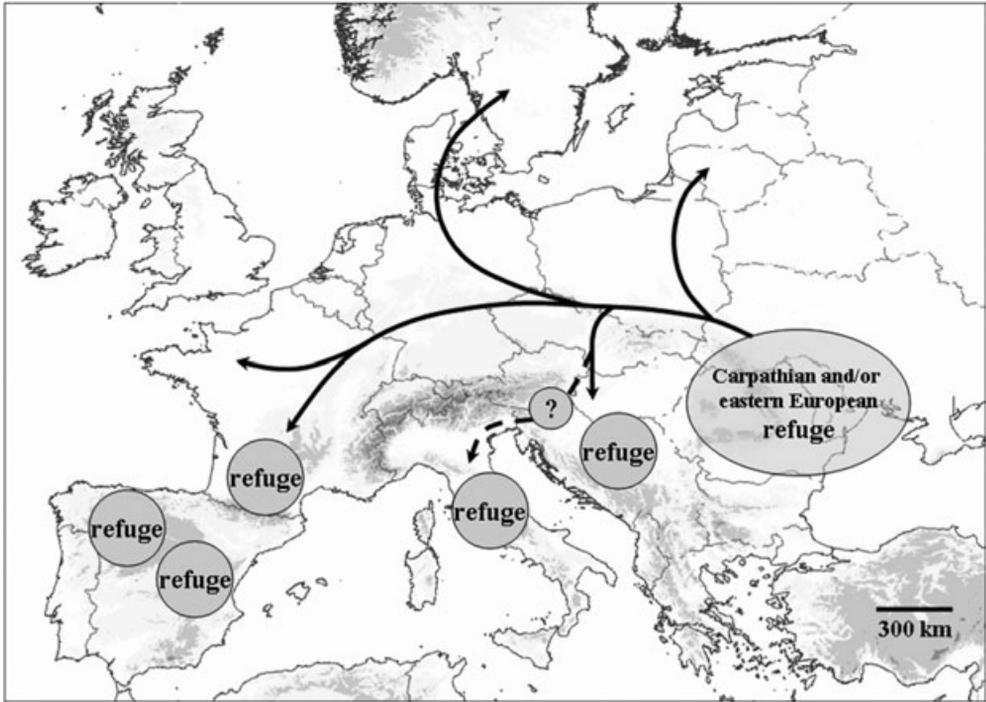


Fig. 6. Hypothesized postglacial recolonization routes of the roe deer out of one or more eastern glacial refugia on the basis of recent genetic and fossil data.

deer in the Carpathian region during the LGM and the early Late Glacial. They also occurred in south-western France at this time, and both the area around the Carpathians and south-western France have been identified as glacial refuges, at least for mammals (Kotlik *et al.*, 2006; Sommer & Nadachowski, 2006).

The hypothesis that roe deer might have recolonized Europe from one or more eastern (not southeastern, i.e. Balkan) refuges, as already considered upon by Lorenzini & Lovari (2006), may in fact best explain the fossil record and the genetic pattern found in extant European roe deer (Fig. 6). In that case, the haplotypes shared between Iberia and Clade Central on the one hand and those shared between the Balkans and Clade Central on the other would have been introduced to the southern regions from the north, not the other way around. The rather high genetic diversity in Iberia and the Balkans would then be the result of admixture in these regions, whereas other authors argued that Clade Central in central-northern Europe was admixed due to the presence of both Iberian and Balkan haplotypes. The scenario presented here would match the fact that there is an isolated eastern clade. If the recolonizing postglacial populations came from the east, then they would have blocked the way north for the Balkan roe deer (Fig. 6). This barrier was probably enforced by the species' pronounced territoriality and could have effectively restricted the Balkan roe deer to the region of their glacial refuge. The phylogenetic position of the eastern clade basal to the other two clades (Randi *et al.*, 2004; Lorenzini & Lovari, 2006) may be interpreted as evidence that these roe deer may even be a relict older than the Weichselian Glacial.

In the west, there were probably two distinct glacial refugia in Iberia (Royo *et al.*, 2007), one in the north-west and one in the central-southern part of the peninsula, plus a refugial area in southwestern France (Fig. 6). Southern Spanish roe deer have sometimes been regarded as a

distinct subspecies *C. c. garganta*, and, similarly to the southern Spanish red deer, they are possibly a mid-Pleistocene relict (Geist, 1998). Two distinct mitochondrial lineages in Iberia have also been found in other mammal species including rabbits (Branco, Ferrand & Monnerot, 2000), red foxes (Fрати *et al.*, 1998) and shrews (Taberlet, Fumagalli & Hausser, 1994). The Pyrenees might have acted as a barrier to a postglacial northward expansion of roe deer. If the postglacial expansion from the Carpathian region or further east also included France and reached Iberia (Fig. 6), thus explaining the occurrence of haplotypes found in both central-northern Europe and in Spain, one would expect a north-south cline in the frequency of Clade Central haplotypes in Iberia. Interestingly, this is exactly what has been found: Royo *et al.* (2007) found a very high proportion of Clade Central haplotypes near the Pyrenees (in Bordeaux, France, and Lleida, Spain), intermediate proportions in north-western and central Spain and no such haplotypes at all in southern Iberia (Cádiz). The same study also yielded haplotypes of the western or Iberian clade in Bordeaux in south-western France, which is in line with the palaeontological evidence for a glacial refuge in this area (Fig. 5).

The nested position within the central-northern European clade of the *C. c. italicus* roe deer (Randi *et al.*, 2004; Lorenzini & Lovari, 2006) suggests that these roe deer are also an offshoot of the eastern immigration wave, but have been isolated since.

The three-clade pattern in the European roe deer that is obvious from both mitochondrial and microsatellite DNA seems inexplicable by a recolonization from an Iberian/SW-French and/or Balkan refuge. All these scenarios would result in a European pattern of two major clades instead of three. Reciprocal monophyly of the three clades (as found in all studies) is expected only after $4N_e$ generations (N_e being the effective population size), a time span much too large to be covered by the time since the last ice age. Consequently, the central-northern European clade is most likely the result of a postglacial immigration wave from one or more eastern refuges, possibly near the Carpathians or further east (Fig. 6). Unfortunately, there are no genetic data from these areas, but if the eastern immigration scenario turns out to be true, these roe deer should unambiguously be assigned to Clade Central. Genetic studies of roe deer from this region and more palaeontological and archaeozoological studies in the east to determine more precisely the geographic extension of the eastern glacial refuge (or refugia) will without a doubt shed further light on the Quaternary history of the European roe deer.

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REFERENCES

- Aaris-Sørensen, K. (2000) Development of the terrestrial mammal fauna in Fennoscandia after the last glaciation. *Lundqua Report*, **37**, 36–44.
- Aragón, S., Braza, F., San José, C. & Fandos, P. (1998) Variation in skull morphology of roe deer (*Capreolus capreolus*) in western and central Europe. *Journal of Mammalogy*, **79**, 131–140.
- Benecke, N. (1999) *The Holocene History of the European Vertebrate Fauna. Modern Aspects of Research*. Marie Leidorf Publisher, Rahden.
- Benecke, N., Bollongino, R., Küßner, M. & Weber, R. (2006) Zur Datierung und Fauna des spätglazialen Schichtkomplexes am Abri Fuchskirche I bei Allendorf, Lkr. Salfeld-Rudolstadt. *Alt-Thüringen*, **39**, 121–130.
- Bilton, D.T., Mirol, P.M., Mascheretti, S., Fredga, K., Zima, J. & Searle, J.B. (1998) Mediterranean Europe as an area of endemism for small mammals rather than a source of northwards postglacial colonization. *Proceedings of the Royal Society London B*, **265**, 1219–1226.
- Bowen, D.Q., Phillips, F.M., McCabe, A.M., Knutz, P.C. & Sykes, G.A. (2002) New data for the last glacial maximum in Great Britain and Ireland. *Quaternary Science Reviews*, **21**, 89–101.

- Branco, M., Ferrand, N. & Monnerot, M. (2000) Phylogeography of the European rabbit (*Oryctolagus cuniculus*) in the Iberian Peninsula inferred by RFLP analysis of the cytochrome b gene. *Heredity*, **85**, 307–317.
- Brunnacker, K., von Koenigswald, W., Rähle, W., Schweingruber, F., Taute, W. & Tille, W. (1977) Der Übergang vom Pleistozän zum Holozän in der Burghöhle von Dietfurt bei Sigmaringen. *Kölner Jahrbuch für Vor und Frühgeschichte*, **15**, 86–164.
- Daniilkin, A.A. (1995) *Capreolus pygargus*. *Mammalian Species*, **512**, 1–7.
- Daniilkin, A.A. & Hewison, A.J.M. (1996) *Behavioural Ecology of Siberian and European Roe Deer*. Chapman and Hall, London.
- Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjörnsdóttir, A.E., Jouzel, J. & Bond, G. (1993) Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature*, **364**, 218–220.
- Eusterhues, K., Lechterbeck, J., Schneider, J. & Wolf-Brozio, U. (2002) Late- and Post-Glacial evolution of Lake Steisslingen (I). Sedimentary history, palynological record and inorganic geochemical indicators. *Palaeogeography Palaeoclimatology Palaeoecology*, **187**, 341–371.
- Frati, F., Hartl, G.B., Lovari, S., Delibes, M. & Markov, G. (1998) Quaternary radiation and genetic structure of the red fox *Vulpes vulpes* in the Mediterranean basin, as revealed by allozymes and mitochondrial DNA. *Journal of Zoology, London*, **245**, 43–51.
- Geist, V. (1998) *Deer of the World. Their Evolution, Behavior and Ecology*. Stackpole Books, Mechanicsburg, PA.
- Gietz, F.J. (2001) *Spätes Jungpaläolithikum und Mesolithikum in der Burghöhle Dietfurt an der oberen Donau*. Konrad Theiss Verlag, Stuttgart.
- Gramsch, B. (2000) Friesack, letzte Jäger und Sammler in Brandenburg. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz*, **47**, 51–102.
- Gronewoudt, B.J., Debben, J., van Geel, B. & Lauwerier, R.C.G.M. (2001) An early Mesolithic assemblage with faunal remains in a stream valley near Zutphen, The Netherlands. *Archäologisches Korrespondenzblatt*, **31**, 329–348.
- Hedges, R.E.M., Pettitt, P.B., Bronk Ramsey, C. & van Klinken, G.J. (1998) Radiocarbon dates from the Oxford AMS system: Archaeometry datelist 25. *Archaeometry*, **40**, 227–239.
- Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, **68**, 87–112.
- Hufthammer, A.K. & Aaris-Sørensen, K. (1998) Late- and postglacial European Roe deer. In: *The European Roe Deer: The Biology of Success* (Ed. by R. Andersen, P. Duncan & J.D.C. Linnell), pp. 47–69. Scandinavian University Press, Oslo, Norway.
- Kaiser, K., Bogen, C., Czakó-Pap, S. & Jahnke, W. (2003) Zur Geoarchäologie des mesolithisch-neolithischen Fundplatzes Rothenklempenow am Latzigsee in der Ueckermünder Heide (Vorpommern). *Greifswalder Geographische Arbeiten*, **29**, 27–68.
- Kotlik, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J.R. & Searle, J.B. (2006) A northern glacial refugium for bank voles (*Clethrionomys glareolus*). *Proceedings of the National Academy of Sciences USA*, **103**, 14860–14864.
- Lehmann, E. & Sägeser, H. (1986) *Capreolus capreolus* Linnaeus, 1758 – Reh. In: *Handbuch der Säugetiere Europas*, Vol. 2/II. Paarhufer, Artiodactyla (Ed. by J. Niethammer & F. Krapp), pp. 233–268. Aula Publisher, Wiesbaden, Germany.
- Lister, A.M., Grubb, P. & Sumner, S.R.M. (1998) Taxonomy, morphology and evolution of European roe deer. In: *The European Roe Deer: The Biology of Success* (Ed. by R. Andersen, P. Duncan & J.D.C. Linnell), pp. 23–46. Scandinavian University Press, Oslo, Norway.
- Litt, T. & Stebich, M. (1999) Bio- and chronostratigraphy of the lateglacial in the Eifel region, Germany. *Quaternary International*, **61**, 5–16.
- Litt, T., Brauer, A., Goslar, T., Merkt, J., Balaga, K., Müller, H., Ralska-Jasiewiczowa, M., Stebich, M. & Negendank, J.F.W. (2001) Correlation and synchronisation of lateglacial continental sequences in northern central Europe based on annually laminated lacustrine sediments. *Quaternary Science Reviews*, **20**, 1233–1249.
- Lorenzini, R. & Lovari, S. (2006) Genetic diversity and phylogeography of the European roe deer: the refuge area theory revisited. *Biological Journal of the Linnean Society*, **88**, 85–100.
- Lorenzini, R., Lovari, S. & Masseti, M. (2002) The rediscovery of the Italian roe deer: genetic differentiation and management implications. *Italian Journal of Zoology*, **69**, 367–379.
- Lorenzini, R., San José, C., Braza, F. & Aragón, S. (2003) Genetic differentiation and phylogeography of roe deer in Spain, as suggested by mitochondrial DNA and microsatellite analysis. *Italian Journal of Zoology*, **70**, 89–99.

- Lõugas, L. (1997) *Post-glacial development of vertebrate fauna in Estonian water bodies. A palaeozoological study*. *Dissertationes Biologicae Universitatis Tartuensiss*, 32, 1–79.
- Ludt, C.J., Schroeder, W., Rottmann, O. & Kuehn, R. (2004) Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Molecular Phylogenetics and Evolution*, **31**, 1064–1083.
- Lundqvist, J. & Saarnisto, M. (1995) Summary of the Project IGCP-253. *Quaternary International*, **28**, 9–18.
- Musil, R. (1980) Die Großsäuger und Vögel von der Täufelsbrücke. *Weimarer Monographien zur Ur- und Frühgeschichte*, **3**, 5–25.
- Musil, R. (2003) The Middle and Upper Palaeolithic game suite in Central and Southeastern Europe. In: *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation* (Ed. by T. van Andel & W. Davies), pp. 167–190. Short Run Press, Exeter, UK.
- Münzel, S., Langguth, K., Conard, N.J. & Uerpman, H.-P. (2001) Höhlenbärenjagd auf der Schwäbischen Alb vor 30.000 Jahren. *Archäologisches Korrespondenzblatt*, **31**, 317–328.
- Niethammer, G. (1963) *Die Einbürgerung von Säugetieren und Vögeln in Europa*. Paul Parey Publisher, Hamburg, Berlin.
- Petit, R.J., Aguinalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J.P., Rendell, S. & Vendramin, G.G. (2003) Glacial refugia: hotspots but not melting pots of genetic diversity. *Science*, **300**, 1563–1565.
- Randi, E., Pierpaoli, M. & Danilkin, A. (1998) Mitochondrial DNA polymorphism in populations of Siberian and European roe deer (*Capreolus pygargus* and *C. capreolus*). *Heredity*, **80**, 429–437.
- Randi, E., Alves, P.C., Carranza, J., Milosevic-Zlatanovic, S., Sfougaris, A. & Mucci, N. (2004) Phylogeography of roe deer (*Capreolus capreolus*) populations: the effects of historical genetic subdivisions and recent nonequilibrium dynamics. *Molecular Ecology*, **13**, 3071–3083.
- Royo, L.J., Pajares, G., Alvarez, I., Fernández, I. & Goyache, F. (2007) Genetic variability and differentiation in Spanish roe deer (*Capreolus capreolus*): a phylogeographic reassessment within the European framework. *Molecular Phylogenetics and Evolution*, **42**, 47–61.
- Rzebik-Kowalska, B. (2003) Insectivores (Insectivora). In: *Oblasowa Cave. Human Activity, Stratigraphy and Palaeoenvironment* (Ed. by P. Valde-Nowak, A. Nadachowski & T. Madeyska), pp. 113–118. Institute of Archaeology and Ethnology Polish Academy of Sciences, Kraków.
- Skog, A., Zachos, F.E., Rueness, E.K., Feulner, P.G.D., Mysterud, A., Langvatn, R., Lorenzini, R., Hmwe, S.S., Lehoczy, I., Hartl, G.B., Stenseth, N.C. & Jakobsen, K.S. Phylogeography of red deer (*Cervus elaphus*) in Europe, submitted.
- Sommer, R.S. & Nadachowski, A. (2006) Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Review*, **36**, 251–266.
- Sommer, R.S., Persson, A., Wiesecke, N. & Fritz, U. (2007) Holocene recolonization and extinction history of the pond turtle, *Emys orbicularis* (L., 1758) in Europe. *Quaternary Sciences Reviews*, **26**, 3099–3107.
- Sommer, R.S., Zachos, F.E., Street, M., Jöris, O., Skog, A. & Benecke, N. (2008) Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe. *Quaternary Science Reviews*, **27**, 714–733.
- Stubbe, M. (1999) *Capreolus capreolus* (Linnaeus, 1758). In: *The Atlas of European Mammals* (Ed. by A.J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Kryštufek, P.J.H. Reijnders, F. Spitzenberger, M. Stubbe, J.B.M. Thissen, V. Vohralik & J. Zima), pp. 400–401. T & A Poyser Natural History Publisher, London.
- Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, G., van der Plicht, J. & Spurk, M. (1998) INTCAL98 radiocarbon age calibration, 24000–0 cal BP. *Radiocarbon*, **40**, 1041–1083.
- Taberlet, P., Fumagalli, L. & Hausser, J. (1994) Chromosomal versus mitochondrial DNA evolution: tracking the evolutionary history of the southwestern European populations of the *Sorex araneus* group (Mammalia, Insectivora). *Evolution*, **48**, 623–636.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. & Cosson, J.-F. (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, **7**, 453–464.
- Taute, W. (1972) Die spätpaläolithisch-frühmesolithische Schichtenfolge im Zigeunerfels bei Sigmaringen (Vorbericht). *Archäologische Information*, **1**, 29–40.
- Usinger, H. (2004) Vegetation and climate of the lowlands of northern Central Europe and adjacent areas around the Younger Dryas – Preboreal transition – with special emphasis on the Preboreal oscillation. In: *Hunters in a Changing World. Environment and Archaeology of the Pleistocene-Holocene Transition (ca. 11 000–9000 B.C.) in Northern Europe* (Ed. by T. Terberger & B.V. Eriksen), pp. 1–26. Marie Leidorf Publisher, Rahden.

- Van Andel, T., Davies, W. & Weninger, B. (2003) The human presence in Europe during the Last Glacial Period I: human migrations and the changing climate. In: *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation* (Ed. by T. van Andel & W. Davies), pp. 31–51. Short Run Press, Exeter, UK.
- Vernesi, C., Pecchioli, E., Caramelli, D., Tiedemann, R., Randi, E. & Bertorelle, G. (2002) The genetic structure of natural and reintroduced roe deer (*Capreolus capreolus*) populations in the Alps and central Italy, with reference to the mitochondrial DNA phylogeography of Europe. *Molecular Ecology*, **11**, 1285–1297.
- Von Koenigswald, W. (1972) Der Faunenwandel an der Pleistozän-Holozän-Grenze in der steinzeitlichen Schichtenfolge vom Zigeunerfels bei Sigmaringen (Vorbericht). *Archäologische Information*, **1**, 41–45.
- Von Koenigswald, W. & Taute, W. (1974) Mensch und Fauna unter dem Einfluß des Klimawandels an der Grenze vom Pleistozän zum Holozän. *Nachrichten der Deutschen Geologischen Gesellschaft*, **9**, 145–150.
- Wiehler, J. & Tiedemann, R. (1998) Phylogeography of the European roe deer *Capreolus capreolus* as revealed by sequence analysis of the mitochondrial control region. *Acta Theriologica*, **5** (Suppl.), 187–197.
- Wille, W. (1981) Die pollenanalytischen Untersuchungen der Burghöhle Dietfurt. In: *Der Übergang vom Pleistozän zum Holozän in der Burghöhle von Dietfurt bei Sigmaringen* (Ed. by K. Brunnacker, W. von Koenigswald, W. Rähle, F. Schweingruber, W. Taute & W. Wille), pp. 98–112. Kölner Jahrbuch für Vor- und Frühgeschichte **15**, Cologne.
- Xiao, C.-T., Zhang, M.-H., Fu, Y. & Koh, H.-S. (2007) Mitochondrial DNA distinction of northeastern China roe deer, Siberian roe deer, and European roe deer, to clarify the taxonomic status of northeastern China roe deer. *Biochemical Genetics*, **45**, 93–102.
- Zachos, F.E., Hmwe, S.S. & Hartl, G.B. (2006) Biochemical and DNA markers yield strikingly different results regarding variability and differentiation of roe deer (*Capreolus capreolus*, Artiodactyla: Cervidae) populations from northern Germany. *Journal of Zoological Systematics and Evolutionary Research*, **44**, 167–174.

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