Phylogeographic, ancient DNA, fossil and morphometric analyses reveal ancient and modern introductions of a large mammal: the complex case of red deer (*Cervus elaphus*) in Ireland

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ABSTRACT

The problem of how and when the island of Ireland attained its contemporary fauna has remained a key question in understanding Quaternary faunal assemblages. We assessed the complex history and origins of the red deer (*Cervus elaphus*) in Ireland using a multi-disciplinary approach. Mitochondrial sequences of contemporary and ancient red deer (dating from *c* 30,000 to 1700 cal. yr BP) were compared to decipher possible source populations of red deer in Ireland, in addition to craniometric analyses of skulls from candidate regions to distinguish between different colonization scenarios. Radiocarbon dating was undertaken on all bone fragments that were previously undated. Finally, a comprehensive review of the scientific literature, unpublished reports and other sources of data were also searched for red deer remains within Irish palaeontological and archaeological contexts. Despite being present in Ireland prior to the Last Glacial Maximum (LGM), there is a notable scarcity of red deer from the Younger Dryas stadial period until the Neolithic. The presence of red deer in Irish archaeological sites then occurs more frequently relative to other species. One population in the southwest of Ireland (Co. Kerry) shared haplotypes with the ancient Irish specimens and molecular dating and craniometric analysis suggests its persistence in Ireland since the Neolithic period. The synthesis of the results from this multi-disciplinary study all indicate that red deer were introduced by humans during the Irish Neolithic period and that one of these populations persists today. In conjunction with recent results from other species, Neolithic people from Ireland's nearest landmass, Britain, played a vital role in establishing its contemporary fauna and flora.

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1. Introduction

The quandary of the colonization of the island of Ireland by its contemporary fauna and flora remains one of the key outstanding questions in understanding Quaternary species assemblages (Moore, 1987; Yalden, 1999; Searle, 2008). Ireland exemplifies the problems associated with islands, namely from where did it attain its contemporary biota, when and by what means. Ireland's geographical position as an outlying island in western Europe presents certain difficulties in terms of how species (including humans) reached it. It could be expected that Ireland would have a relatively similar faunal and floral assemblages to that of Britain given the proximity of these two large islands, yet many species are absent from Ireland that are commonly found in Britain (the common shrew (*Sorex araneus* Linnaeus, 1758), field vole (*Microtus agrestis* Linnaeus, 1761) and European roe deer (*Capreolus capreolus* Linnaeus, 1758) for example; Yalden, 1999). This has led to considerable debate about putative glacial refugia (Provan et al., 2005; Teacher et al., 2009), natural colonization via land or ice bridges (Hamill et al., 2006; Martínková et al., 2007) and

anthropogenic introductions (McDevitt et al., 2011). Most of our present knowledge regarding Irish colonization processes comes from studies of mammals (both in terms of fossils and phylogeographic studies), so it is perhaps surprising then that the history of Ireland's largest and arguably its most iconic terrestrial mammalian species, the red deer (*Cervus elaphus* Linnaeus, 1758), has remained relatively unexplored.

Red deer is one of only three species of Cervidae found in Irish archaeological sites pre-13th Century contexts and is the only one of those species still extant in Ireland (Woodman et al., 1997); the giant deer (*Megaloceros giganteus* Blumenbach, 1803) and reindeer (*Rangifer tarandus* Linnaeus, 1758) disappeared during the Late Glacial or early Holocene period prior to the arrival of humans to Ireland (10,155−9531 cal. yr BP, Mount Sandel, Co. Derry; Woodman, 1985; Bayliss and Woodman, 2009). The three other species of deer that currently reside in Ireland (European fallow deer (*Dama dama* Linnaeus, 1758), sika (*Cervus nippon* Temminck, 1838) and Reeves' muntjac (*Muntiacus reevesi* Ogilby, 1839)) were all certainly deliberate human introductions within historical times (Carden et al., 2011) as were the European roe deer which were introduced to Lissadell, Co. Sligo in the early 1870s from Dupplin Estate, Perthshire, Scotland but were shot out in the early 1900s (Whitehead, 1964).

Red deer had a wide geographical distribution within the European Late Quaternary period (Sommer et al., 2008). During the Last Glacial Maximum (LGM), the time at which the ice sheets were at their maximum extension *c* 26,500−19,000 cal. yr BP (Clark et al., 2009, 2010), red deer were entirely absent from Northern Europe (Sommer et al., 2008). The ice-sheet(s) may have covered much, if not all, of the island of Ireland (Coxon and McCarron, 2009; Chiverrell and Thomas, 2010; Ó Cofaigh et al., 2011). After such an extensive glaciation, whether or not a putative land- or ice-bridge(s) existed for a short time post-LGM (see discussions in Devoy, 1985; Wingfield, 1995; Edwards and Brooks, 2008) is somewhat irrelevant. The presence, or indeed the absence, of a land-bridge does not universally explain why only certain mammalian species are found in Ireland before the arrival of humans (Woodman et al., 1997). The Irish Late Quaternary fossil record derived from numerous palaeontological (mainly cave sites) and archaeological contexts has been subjected to an extensive ^{14}C AMS radiocarbon dating programme by Woodman et al. (1997). This programme found two red deer specimens from two separate caves, Shandon and Ballynamintra located in the southeast of Ireland that dated to pre-LGM (32,930−29,594 cal. yr BP, Appendix S2). There appears to be a paucity overall of red deer in Ireland prior to the LGM. Reindeer skeletal remains as well as other species such as mammoth (*Mammuthus primigenius* Blumenbach, 1799) are more frequently found in these contexts (see Woodman et al., 1997). Furthermore, only one dated specimen from the late glacial was identified and dated, while none of the specimens dated to the Holocene, *i.e.* after 11,600 cal. yr BP, predate the Neolithic. Therefore it has been suggested that red deer were introduced at some stage after the human colonization of Ireland (Woodman et al., 1997; McCormick, 1999; Yalden, 1999).

Irish red deer populations are not currently widely distributed over the island of Ireland (see Carden et al., 2011), but they still occur in three original 'stronghold' areas of the 1800s, namely, the counties of Wicklow, Donegal and Kerry (Fig. 1a) as noted by Whitehead (1960). Other smaller populations are found in at least 10 other counties (see Carden et al., 2011). The 12th Century historian Giraldus Cambrensis noted during his travels around Ireland the presence of very low numbers of deer in Ireland (Cambrensis, 1183-1185). Historical documentation has recorded translocations of red deer from other countries as well as movement within the island of Ireland (Moffat, 1938). From the 1600s

onwards, there are reports of small numbers of red deer in forests in the south and east of Ireland (Ryan, 2001). Further importation of red deer from the Island of Islay, Scotland to the Powerscourt Demense in Co. Wicklow occurred during the late 1800s (Whitehead, 1960). In 1891 when the Glenveagh Forest in Co. Donegal was enclosed by a deer fence, various translocations from Scotland, England and other parts of Ireland occurred until 1949 (Whitehead, 1960). Further introductions occurred into the north-west during the 19th Century with red deer brought in from various British deer parks (Whitehead, 1960). More recently during the early 1980s, deer from continental European stock and Warnham Park, Sussex, UK were translocated to a privately owned, un-enclosed estate in Connemara, Co. Galway (McDevitt et al., 2009a).

There is a paucity of historical records for red deer in the Co. Kerry region other than historical references to low numbers of red deer occurring near Killarney, Co. Kerry (Thompson, 1856; Ussher, 1882; Scharff, 1918). There have been documented introductions of small numbers of red deer stags from Co. Roscommon (1870s), Windsor Great Park, England (1 stag *c* 1900) and Scotland (*c* early 1900s; Whitehead, 1960; Ryan, 2001). Concurrently, during the late 1800s/ early 1900s, unknown numbers of Killarney red deer stags were being translocated to Scotland (Isle of Mull, Isle of North Uist and the Isle of Jura) and at least 11 stags and two hinds were transported to Co. Roscommon and unknown numbers to Co. Donegal (Whitehead, 1960). All of these translocations would have involved the transportation of male and female red deer (Whitehead, 1960).

In this study, we used a multi-disciplinary approach to examine the history of red deer in Ireland because the complex mechanisms by which Ireland was colonized by faunal species are difficult to address within a single discipline, particularly when humans are involved (see McDevitt et al., 2011). We began by undertaking a comprehensive review of the scientific literature. Unpublished reports and other sources of data were searched for any mention of red deer skeletal remains within Irish palaeontological and archaeological contexts and sites. We then utilized a large number of contemporary tissue samples from Ireland, Britain, New Zealand and continental Europe, as well utilizing ancient DNA (aDNA) from Irish bone fragments (ranging in age from approximately 30,000 to 1700 cal. yr BP) in phylogeographic and molecular dating analyses to describe the genetic relationships between modern and ancient Irish samples with those from elsewhere. Radiocarbon dating was undertaken on all bone fragments that were previously undated so significantly increasing the amount of data which had previously been available and published (see Materials and Methods). Finally, in light of the results obtained from the genetic analyses and historical records of introductions, we subjected female adult skulls from candidate regions to craniometric analyses in order to distinguish between different colonization scenarios.

2. Materials and methods

2.1. DNA analysis

2.1.1. Contemporary samples

Genomic DNA was extracted from 172 contemporary individuals (81 Irish and 91 individuals from Britain, continental Europe and New Zealand; see Appendix S1 in the Supporting Information) using tissue samples of muscle or ear stored in 100% ethanol obtained from deer stalkers or rangers, either using the ZR Genomic DNA II Kit (Zymo Research) according to the manufacturer's protocol, or a simple salting-out procedure (Miller et al., 1988). One-sample of hair and tissue sample came from a mounted red deer trophy labelled as having been shot in Otago, New Zealand in 1903. This sample was treated as ancient and extracted and ana-lysed as noted below. We also obtained modern samples directly
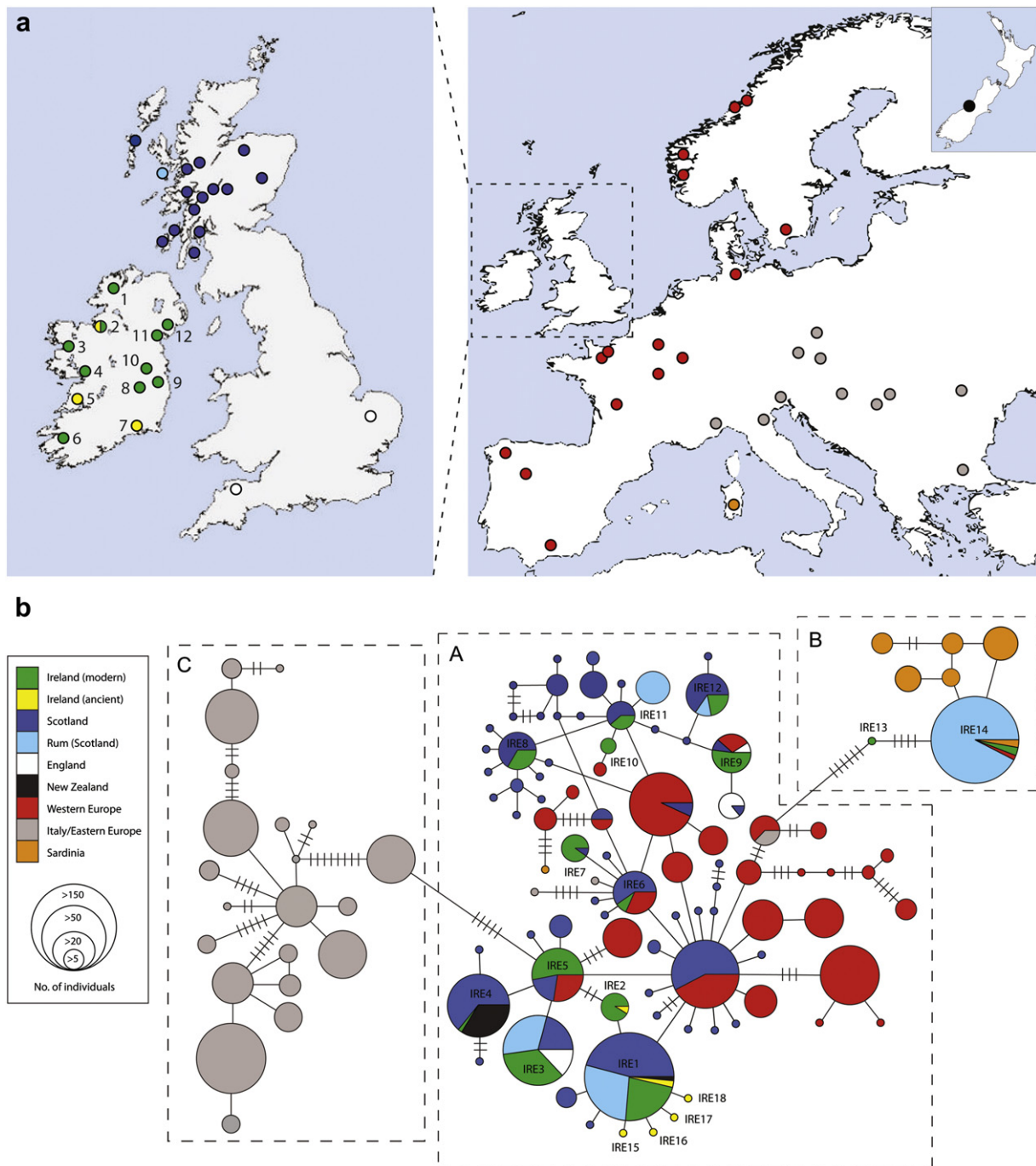
Fig. 1. Map of Europe (with New Zealand inset) showing (a) geographic origin of samples and (b) MJ network of control region haplotypes. In the network, circles represent haplotypes and size corresponds to the number of individuals having that particular haplotype. Vertical lines represent mutational steps when greater than one. Haplotypes found in Ireland are labelled IRE1-18. The network is split into the three main haplogroups (A, B and C) known from previous studies of European red deer (for details, see Results). Important Irish populations referred to in the text are numbered in (a): 1. Co. Donegal; 2. Co. Sligo/Fermanagh; 3. Co. Mayo; 4. Co. Galway; 5. Co. Clare and 6. Killarney National Park, Co. Kerry; 7. Co. Waterford; 8. Co. Kildare; 9. Co. Wicklow; 10. Co. Meath; 11. Co. Louth and 12. Co. Down.

from the Westland and Otago regions in New Zealand as these deer (particularly those from Otago) may be the descendants of "indigenous Scottish red deer (*C. e. scoticus*)" because it has been proposed that admixture of deer from English parks and other sources has since taken place in Scotland (Banwell, 1994). Seventeen young red deer (fifteen of which survived) were captured in Invermark Forest, northeast Scotland and were translocated by ship in two different lots and released in the Otago region of the South Island, New Zealand in 1870/71 (Druett, 1983).

The entire control region (mitochondrial DNA) was amplified using the primers CE-CR-FOR and CE-CR-REV (McDevitt et al., 2009a) according to the protocol described in McDevitt et al. (2009a). In order to compare our data with 1208 previously published sequences from Ireland, Britain and continental Europe (Appendix S1), the whole control region was truncated to the most informative 332 base pairs (bp) section. The region analysed was a defined, highly variable region of the mtDNA control region between bases 15,587 and 15,918. In total, 165 Irish, 532 Scottish, 17

English, 647 continental European and 19 (including one historic) New Zealand contemporary individuals were used in this study, giving a total modern mitochondrial dataset of 1380 red deer (Appendix S1).

2.1.2. Ancient samples

We collected skeletal elements of 23 putative *C. elaphus* samples from 15 sites in Ireland (Appendix S2). Appropriate procedures were followed for the handling and analysis of ancient specimens during all steps of the DNA extraction and amplification procedure (Greenwood and Pääbo, 1999; Cooper and Poinar, 2000; Gilbert et al., 2005). DNA was extracted in the specialised ancient DNA facilities at the Smurfit Institute of Genetics, Trinity College, Dublin, following the protocol described in Edwards et al. (2010). PCR set-up was conducted in a laboratory dedicated solely to pre-amplification ancient work. To overlap with the modern data, three overlapping fragments of 159 bp, 155 bp and 149 bp of the hypervariable section of the mitochondrial control region were designed by aligning mitochondrial genomes found in GenBank. The primers were, by necessity, degenerate in nature due to the small number of available sequences from red deer when our study began, and are as follows: RD1F (5′-CCA CYA ACC AYA CRA CAR AA-3′) and RD1R (5′-TTR TTT AYA GTA CAT AGT RCA TGA TG-3′); RD2F (5′-GCC CCA TGC WTA TAA GCA TG-3′) and RD2R (5′-CCA TGC CGC GTG AAA CCA-3′); RD3F (5′-GAT CAC GAG CTT GRT YAC C-3′) and RD3R (5′-TTC AGG GCC ATC TCA CCT AA-3′). PCR conditions were as described in Stock et al. (2009), but with the following annealing temperatures: RD1F–RD1R = 52 °C; RD2F–RD2R = 54 °C; RD3F–RD3R = 53 °C.

Amplicons were sequenced in both directions, and PCR products were cleaned using the QIAquick PCR Purification Kit (Qiagen) according to the manufacturer's instructions, but with an additional wash step. Two separate batches of purified PCR products were Sanger-sequenced commercially by Macrogen Inc., Korea. Two of the 23 samples (RD12 and RD14) were independently replicated at Cambridge, following the protocol described by Campana et al. (2010), using the primer set RD1F–RD1R and conditions as above. Independent replication revealed minimal levels of DNA damage. In addition, no amplification products were observed either in extraction or amplification negative controls. In total, 12 out of 23 samples (52.2%) were successfully amplified.

2.1.3. Genetic analysis

The total sequence length used in all genetic analyses was 332 bp, except where noted for ancient DNA specimens (Appendix S2). This allowed direct comparisons to previously published data on *C. elaphus* control region sequences. Genetic variability was calculated as haplotype and nucleotide diversity using DnaSP v. 5 (Librado and Rozas, 2009). A phylogenetic network was constructed from all contemporary and ancient sequences using the software Network version 4.6 (www.fluxus-engineering.com) with a Median-Joining (MJ) algorithm (Bandelt et al., 1999). Simulation studies have demonstrated that this method provides reliable estimates of the true genealogy (Cassens et al., 2005).

We wished to compare the modern Killarney National Park red deer from Co. Kerry with their putative ancestors (the ancient individuals from Ireland) and to estimate the changes in population size through time. Unfortunately, due to the low level of variation seen in these individuals, it was not possible to run a coalescent-based approach that took the sequence ages of the ancient data into account. There was insufficient information available to estimate the rate and timescale and, therefore, the data did not pass the randomisation test described in Ho et al. (2011); a test which involves the analysis of a number of replicate data sets in which the ages of the sequences are shuffled. For the 'Co. Kerry + ancient' data set, the randomised replicates gave the same rate estimate as the original data set, implying that the sequence ages and the sequence data were not sufficiently informative. In addition, no support was found for a demographic model more complex than constant population size through time.

In order to date the time to the most recent common ancestor (TMRCA) of the 52 modern Co. Kerry deer (see Results), the rho (ρ) statistic (Forster et al., 1996) was used as an unbiased estimator of the coalescence time depth within the Co. Kerry red deer. This was calculated by dividing the number of mutational steps from the central haplotype ($n = 11$) by the total number of samples in this group ($n = 52$), to give a ρ equal to 0.2115. Pitra et al. (2004) estimated the rate of nucleotide substitution in the *Cervus* cytochrome *b* gene to be 5.14% per Myr. As Skog et al. (2009) found the relative rate difference between coding (cyt*b*) and non-coding (control region) regions in red deer to be 2.7, we determined the evolutionary rate for the control region as 13.878% per Myr. However, this rate is very approximate as it does not take into account the associated estimation error and, therefore, the date estimates obtained using this assumed rate will most likely be over-estimations as various factors tend to cause rates among species to be lower than rates within species (Ho and Larson, 2006). In addition, care must be taken as the mutation rate might also signify a possible underestimation as the fossil calibrations used by Pitra et al. (2004) represent minimum bounds. In any case, we were aware of the limitations of this method, but used it in order to give an indication of the time since divergence. This was calculated using the mutation rate and the rho statistic, along with a 95% central credible region, in the program CRED (Macaulay, 1998).

2.2. Radiocarbon dating

Six of the 23 Irish deer had been dated previously as part of The Irish Quaternary Fauna Project (Woodman et al., 1997) (OxA dates; Appendix S2). AMS radiocarbon dates were generated for the 17 additional Irish samples by the [14]Chrono Centre, Queen's University Belfast (UB dates; Appendix S2). Stable isotope analysis was carried out as part of the dating process, either by ORAU or Chrono QUB (OxA and UB numbers respectively; Appendix S2). In addition, three red deer from the ORAU online database, plus one unpublished red deer (M. Dowd, Sligo Institute of Technology, Ireland, personal communication 2011), with accompanying radiocarbon dates (and their respective associated δ^{13}C and δ^{15}N stable isotope data), were included in the analyses. The radiocarbon dates are reported as calibrated years before present (cal. yr BP), at the 2-sigma (δ) precision. CALIB Rev 6.0.1 (www.calib.org) was used to calibrate the dates (Stuiver and Reimer, 1993).

2.3. Craniometrics and statistical analyses

A small sample of 55 adult female red deer skulls (see Appendix S3 for specimen list and origins) from three candidate populations were either specifically collected or measured in various museum collections. Table 1 provides the anatomical descriptions for each of the eight measurements recorded from the skulls that were derived from holdings of modern collections within National Museums of Scotland, Edinburgh ($n = 20$), National Museum of Ireland, Natural History Division (Co. Kerry, $n = 26$) and from the personal collections of R.F. Carden (Co. Donegal, $n = 9$). No adult female skulls, fragmentary or whole, were identified in the NMI collections from archaeological and palaeontological specimens.

These specific populations were chosen to examine if the proposed 'ancient' Irish population (Co. Kerry) was distinct from both a 'modern' Irish population (Co. Donegal) and its proposed source population (Scotland; see Results). Adult skulls were defined by fully fused cranial sutures and fully erupted and in-wear

Table 1
Anatomical descriptions of the eight craniometric data recorded. Measurements (mm) as per von den Driesch (1976).

Measurement	Description
M3	Basal length: Basion − Prosthion
M5	Premolare − Prosthion
M10	Median frontal length: Akrokranion − Nasion
M19	Lateral length of the premaxilla: Nasointermaxillare − Prosthion
M26	Greatest breadth of the occipital condyles
M32	Greatest breadth across the orbits: Ectorbitale − Ectorbitale
M33	Least breadth between the orbits: Entorbitale − Entorbitale
M36	Greatest breadth across the premaxillae

maxillar cheek teeth (Brown and Chapman, 1991). These skulls permitted the recording of craniometric data using stainless steel 150 mm digital callipers (accurate to 0.03 mm) and a metal 3 m tape measure (accurate to 1 mm). Mature female skulls were chosen as female red deer tend to be shot non-selectively and were preferred over adult male skulls due to the additional complication of antlers affecting the shape of the skull. Four (two Scottish and two from Co. Kerry) of the 55 skulls had missing data due to damaged skulls and thus had to be omitted from the multivariate analyses. The comparable mean measurements from adult female skulls derived from Glenveagh, Co. Donegal (Murphy, 1995) were used in the craniometric analyses (raw data were unavailable); these measurements were based on a sample size of 28 skulls and all mean measurements were within our Donegal sample range. All measurements recorded were as per von den Driesch (1976). To test for measurement errors, five skulls were randomly selected and each measurement recorded five times on each skull. The coefficient of variation for each variable was calculated (Lynch et al., 1996) (data not shown). Variables with a mean coefficient of variation of more than 2% were excluded from further analyses; none of the 33 measurements initially used were excluded (Appendix S4).

Table 2
Irish haplotypes and the localities in Ireland, Britain, continental Europe and New Zealand in which they are found (See Fig. 1b for Irish haplotypes). The number of individuals from each locality is indicated in parentheses when greater than one.

Haplotype	Localities found
IRE1	Killarney (41), Co. Donegal (24), Co. Galway, Co. Sligo, Co. Clare (aDNA; 2432−2118 cal. yr BP), Co. Waterford (aDNA; 2770−2740, 2782−2722, 3340−3082 cal. yr BP), Rum (Scotland; 49), Scotland (36), New Zealand
IRE2	Killarney (11), Co. Waterford (aDNA; 30,297-29,594 cal. yr BP)
IRE3	Co. Donegal, Co. Down (4), Co. Galway (5), Co. Kildare (2), Co. Louth, Co. Meath, Co. Mayo (7), Co. Wicklow, England (15), Rum (Scotland; 21), Scotland (5)
IRE4	Co. Mayo, Scotland (34), New Zealand (18)
IRE5	Co. Donegal (16), Co. Mayo (2), Co. Sligo, Scotland (7), France (10)
IRE6	Co. Mayo, Co. Sligo, Scotland (15), Norway (7), Spain
IRE7	Co. Fermanagh, Co. Galway (5), Co. Sligo, Co. Wicklow (2), Scotland
IRE8	Co. Donegal, Co. Mayo (5), Scotland (12)
IRE9	Co. Galway (10), Co. Sligo, Scotland (2), England (2), France (6)
IRE10	Co. Galway (3)
IRE11	Co. Galway (3), Co. Mayo, Scotland (6)
IRE12	Co. Donegal (5), Rum (Scotland; 2), Scotland (16)
IRE13	Co. Wicklow
IRE14	Co. Wicklow (5), Rum (Scotland; 190), Sardinia (4), Spain
IRE15	Co. Sligo (aDNA; 2121−1996 cal. yr BP)
IRE16	Co. Waterford (aDNA; 2954−2809 cal. yr BP)
IRE17	Co. Waterford (aDNA; 1987−1883 cal. yr BP)
IRE18	Co. Clare (aDNA; 1862-1705 cal. yr BP)

The initial principal component analysis reduced the 33 measurements down to eight, which adequately explained most of the variation (size and shape) between the three populations and only results from these are reported hereafter.

Prior to analysis, all data were transformed to logarithmic base 10 (log_{10}) and all data were screened prior to analyses. The distributions of all data were investigated prior to all analyses using the one-sample Kolmogorov−Smirnov test and graphical examination of each variable was performed (for further statistical details see Carden (2006)). Univariate and multivariate analyses were performed with statistical significance accepted at a two-tailed 0.05 level (Sokal and Rohlf, 1995). All measurements are given in millimetres (mm). PASW Statistics version 18.0.2 (SPSS Inc., 2010) was used for all statistical analyses.

It has been suggested that the shape of the cervid skull may be genetically determined, in accordance with pre-determined growth and developmental patterns, despite malnutrition effects (Lowe and Gardiner, 1974; Carden, 2006). This was investigated, subsequent to the PCA analyses, using a discriminant function analysis based on a jackknife classification procedure, to quantify the separation of the three populations of red deer crania with respect to the degree of morphometric similarity.

3. Results

3.1. Records of red deer remains

A comprehensive review of the palaeontological and zooarchaeological Irish sites is presented in Appendix S5. Included in this table are the few published Irish Mesolithic sites, which highlights the absence of red deer remains (antler or bone) recorded at that period of time. Many of the sites mention the presumed presence of red deer rather than actual material detected in the assemblages. Overall, given the absence of red deer remains from a range of Mesolithic sites, there is at the moment no clear or unequivocal evidence that this species was present in Ireland throughout the earliest part of the Holocene, including throughout the Mesolithic, until the introduction of farming about 5800 cal. yr BP. Evidence from the Early and Middle Neolithic (i.e. down to 4700 cal. yr BP) is quite sparse, with between less than 1%−3% of red deer skeletal/antler remains relative to other species present such as cattle, sheep/goat and pig. Depending on the specific site or context these figures represent between one individual deer, or part thereof, to fewer than 10 deer overall. No red deer remains have been recovered from Court or Portal Tombs in Ireland (Woodman et al., 1997); in contrast, several passage tombs have produced numerous pins that have been fashioned from antler fragments.

In summary, it is clear from the review that the presence of red deer in Irish sites occurs more frequently as fragments (either worked or not) of antler material rather than skeletal remains (postcranial) and, where such are present, they are relatively sparse and few in number relative to other species.

3.2. Genetic data

Reliable sequence data was obtained from all contemporary samples (including the single New Zealand individual supposedly shot in 1903). Haplotype and nucleotide diversities of the Irish populations are given in Appendix S6. Partial sequence data was obtained from 12 out of the 23 ancient specimens, ranging in size from 76 to 332 bp (Appendix S2). Of the 13 samples from cave sites, 12 gave reliable amplifiable DNA; a success rate of over 92%. The remaining 10 samples were from non-cave sites, which were expected to have a lower success rate, including lake shore settlements, a peat bog and a beach (see Appendix S2 for more details).

None of these non-cave remains yielded any ancient DNA, which was unsurprising in the main, although it was expected that perhaps the antler from the anoxic waterlogged site of Fishamble Street, Dublin, might allow for DNA amplification, given an almost 65% success rate previously seen in cattle from the site (MacHugh et al., 1999). Sequences obtained from ancient specimens were BLAST-searched to determine whether or not they were identified correctly as *C. elaphus* bone fragments. It was found that three of these specimens (all pre-LGM specimens) were in fact reindeer (*R. tarandus*) (Appendix S2; Genbank Accession Nos.: JQ599378–JQ599380).

Phylogenetic analysis in Network corresponded to the three main haplogroups known from European red deer (Skog et al., 2009; Niedziałkowska et al., 2011; Zachos and Hartl, 2011). Haplogroups were formed from individuals mainly from the British Isles and Western Europe (lineage A); individuals mainly from Sardinia and Rum (lineage B) and, finally, individuals from Italy and Eastern Europe (lineage C; Fig. 1b). A total of 115 *C. elaphus* haplotypes were found in 1389 individuals (modern and ancient). Eighteen haplotypes were found in Ireland (IRE1–18; Fig. 1b, GenBank Accession Nos.: JQ599359–599376), of which seven were unique to the island (incorporating a total of 15 contemporary and five ancient individuals; Fig. 1b). All other Irish individuals shared haplotypes with Scottish individuals (both mainland and the island of Rum) and, in certain cases, additionally with individuals from England, France, Norway, Spain and New Zealand (Fig. 1b). Haplotype IRE1 was found in four Irish contemporary locations (Cos. Donegal, Galway, Kerry and Sligo), Scotland, Rum and a solitary individual from New Zealand, as well as in four ancient Irish individuals ranging in age from 3340 to 2118 cal. yr BP (RD12, RD21, RD24, RD26; Table 2, Appendix S2). All other ancient Irish individuals differed from this haplotype by a single bp (Fig. 1b). Haplotypes IRE15–18 ranged in age from 2954 to 1705 cal. yr BP (RD03, RD05, RD17, RD22; Table 2, Appendix S2). The oldest dated Irish specimen, and only pre-LGM specimen that yielded a control region sequence corresponding to *C. elaphus* (30,297–29,594 cal. yr BP (RD23); Table 2, Appendix S2), had the same haplotype (IRE2) as contemporary individuals found in Co. Kerry.

IRE3 was found in eight counties in Ireland (spread out in the western, northern and eastern parts of the island) and was shared with individuals from Scotland, Rum and England. Haplotypes IRE4–12 were all northwestern (Cos. Donegal, Fermanagh and Sligo) and western (Cos. Galway and Mayo) Irish individuals and shared haplotypes mainly with Scottish individuals but also some European populations (Fig. 1b, Table 2).

From an Irish perspective, haplotypes IRE13 and IRE14 were found only in Co. Wicklow in the east. IRE13 was a singleton and differed from the nearest haplotype by 4 bp, being somewhat intermediate between lineages A and B (Fig. 1b). IRE14 was found in five individuals from Co. Wicklow. This was the most abundant haplotype found in Rum and is clearly part of the Rum–Sardinia haplogroup (Fig. 1b).

The TMRCA within the Co. Kerry red deer cluster (haplotypes IRE1 and 2) was calculated using the statistic rho, the mean number of mutations from the central founder sequence to lineages within each cluster. This gives an unbiased estimate, and a central 95% credible interval (CI) may be calculated assuming a true star-like phylogeny and a Poisson distribution for the mutational process (Richards et al., 2000). Although the Co. Kerry red deer phylogeny is not a true star-like phylogeny, having only two haplotypes separated by a single base pair mutation, this calculation allows us an impression of the approximate time period that the Co. Kerry deer were introduced into Ireland. The approximate estimate of the TMRCA of the Co. Kerry deer was 4901 cal. yr BP, with a 95% CI of between 2447 and 8194 cal. yr BP.

3.3. Radiocarbon AMS dating

The radiocarbon dates from, positively identified, red deer skeletal remains from a wide range of Irish contexts are presented in Appendix S2. Red deer skeletal samples were chosen arbitrarily from sites in which they occurred, rather than a specific geographical, temporal or spatial pattern. Two red deer specimens were dated to pre-LGM: 30,297–29,594 cal. yr BP (UB-14770 (RD23; Appendix S2); this study) and 32,930–31,280 cal. yr BP (OxA-4366; Woodman et al., 1997). Excluding the samples identified as reindeer (see genetic data), both were from County Waterford caves in the southeast of Ireland. There is a single specimen of red deer dated to the Late Glacial period from a cave in the northwest of Ireland, 13,883–13,375 cal. yr BP (OxA-3693 (RD13; Appendix S2); Woodman et al., 1997). There is, then, a noticeable time gap between *c.* 13,880 to 4871 cal. yr BP in which no red deer remains have been dated in Ireland, and from the Later Neolithic period (*c.* 4500 cal. yr BP) there are clusters of dates from various locations and contexts (Fig. 2, Appendix S2).

3.4. Craniometric analyses

3.4.1. Principal component analysis

The means, standard deviations and the ranges of the eight measurements of the 55 skulls, split per population group (Cos Kerry and Donegal, Ireland and Scotland), are presented in Appendix S7. A PCA analysis was run based on a correlation matrix with an orthogonal (varimax) rotation to investigate population differences between the adult female skulls from Scotland, Cos. Kerry and Donegal. Overall, the first component (PC1) accounted for just over 25% of the variation, while the second component (PC2) accounted for nearly 17% of the variation (Appendix S8). The first and second principal components and their positive weightings can be largely ascribed to the overall larger skull size of Co. Kerry red deer relative to the Co. Donegal and Scottish populations; that is, the measurements that correspond to the inter-orbital breadth (M32, M33) relative to the ventral length of the skull (M3, M5). Examination of the remaining components and their respective weightings and scores of the four analyses revealed various high positive weightings to different measurements pertaining to breadths and lengths of the skulls (*i.e.* less size and more shape influences; data not shown). The six components were subjected to a univariate analysis (One-Way ANOVA) with the sequential Bonferroni correction for multiple comparisons. This revealed a significant difference between the three red deer populations present in PC1 (Univariate $F_{2,49} = 20.081$, $P < 0.001$), PC3 (Univariate $F_{2,49} = 4.945$, $P < 0.05$) and PC6 (Univariate $F_{2,49} = 15.020$, $P < 0.001$), but not for PC2 (Univariate $F_{2,49} = 0.448$, $P = 0.641$), PC4 (Univariate $F_{2,49} = 1.135$, $P = 0.335$) or PC5 (Univariate $F_{2,49} = 3.089$, $P = 0.055$ (although this is approaching significance)). Three measurements in particular (M3, M10 and M26; high loadings on PC3 and PC5; Appendix S8) influenced the degree of separation or similarity between the Co. Kerry, Scottish and Co. Donegal red deer skulls, whereby the Co. Kerry red deer skulls displayed separation, but not fully, from the Scottish and Co. Donegal skulls based on the combined skull length and occipital condylar width measurements (shape) (Fig. 3).

3.4.2. Discriminant function analysis

A discriminant function analysis was run based on the two principal component scores (PC3 and PC5) from the three-population PCA analysis. The DFA (Appendices S9, S10) correctly classified 16/24 of the Co. Kerry, 8/18 of the Scottish and 0/10 of the Co. Donegal female red deer skulls (Appendix S9) (Function 1: Wilks' $\lambda = 0.731$, $\chi^2 = 15.170$, d.f. $= 4$, $P < 0.005$; Function 2: Wilks'
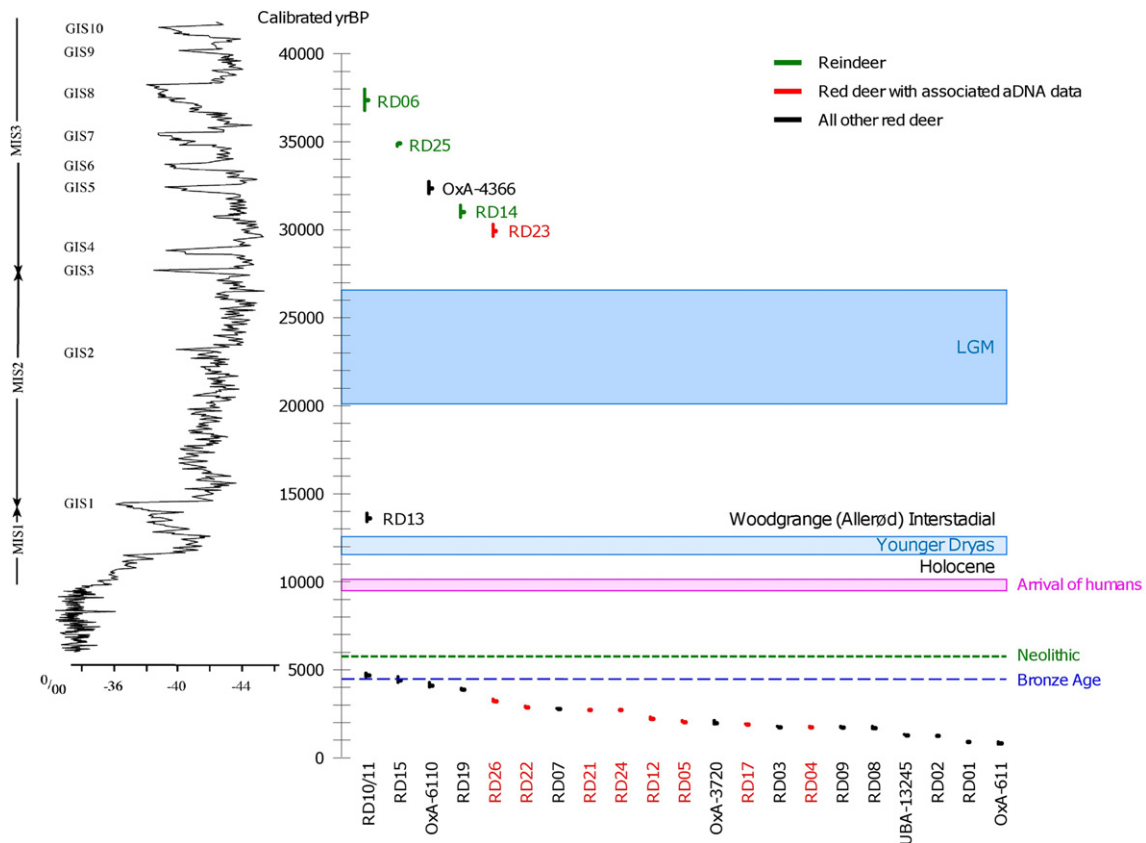
Fig. 2. Radiocarbon date timeline for all dated red deer samples from Ireland. Plotted against the oxygen isotope curve from NGRIP (in ‰) and using the GICC05 timescale (in thousands of years before the year 2000; Lowe et al., 2008). The main Greenland Interstadial and Stadial events for the time period are shown. The LGM period denoted is that at which the ice sheets were at their maximum extension c. 26,500–19,000 cal. yr BP (Clark et al., 2009; Clark et al., 2010).
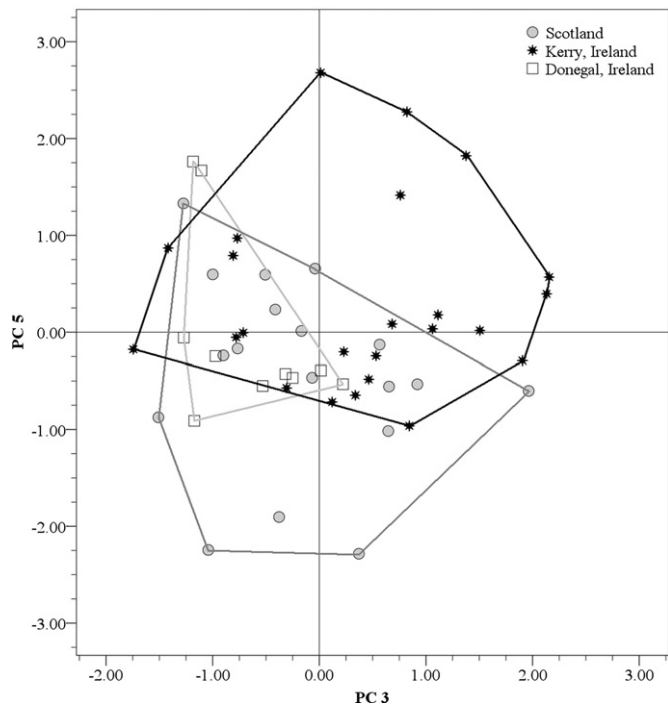

Fig. 3. Distribution of the shape of the Scottish, Donegal and Kerry adult female red deer skulls in accordance with the third and fifth principal components scores.

$\lambda = 0.951$, $\chi^2 = 2.436$, d.f. $= 1$, $P = 0.119$). Of the cross-validated grouped cases, 46.2% were correctly classified. Eight of the Scottish were classified as part of the Co. Kerry population and a further two Scottish red deer skulls were classified as Co. Donegal. None of the Co. Donegal red deer skulls were correctly classified to their population: two were classified as Co. Kerry and eight as Scottish. Sixteen of the Co. Kerry red deer skulls were correctly classified, with a further two classified as Co. Donegal and six as Scottish (Appendix S9).

4. Discussion

The 'Irish Question' remains a key question in biogeographic faunal studies over the past few decades (Moore, 1987; Yalden, 1999; Searle, 2008). The advent of molecular techniques has allowed a greater understanding of how mammals, in particular, colonized Ireland (Searle, 2008). However, the complex means by which mammals reached Ireland are difficult to address using molecular data alone, and this is particularly true when humans are involved, whether these are deliberate or accidental introductions (McDevitt et al., 2011). This is especially relevant for an animal such as the red deer, which has a long history of being translocated by humans (Zachos and Hartl, 2011). To address this question of the Irish origins of this species and advance our knowledge in terms of the colonization of Ireland, we have used a multi-disciplinary approach that provides a synthesis of work involving historical and archaeofaunal records and data, AMS radiocarbon dating series and molecular-based techniques, in conjunction with craniometrics.

Phylogeographic analysis identified the three main lineages based on haplogroups previously identified from European red

deer: Rum–Sardinia (equivalent to North-Africa/Sardinia in previous studies), the British Isles-Western Europe and Italy-Eastern Europe (Fig. 1b; Niedziałkowska et al., 2011; Zachos and Hartl, 2011). We identified 115 haplotypes within the total set of 1389 sequences, of which 18 haplotypes were found in Ireland (IRE1–18; Fig. 1b; Table 2). Eleven of these 18 Irish haplotypes were shared between various Irish populations (Cos Donegal, Galway, Sligo, Down, Kildare, Louth, Meath, Mayo, Wicklow, Fermanagh and Kerry) as well as red deer from Scotland, England, continental Europe and New Zealand (IRE1, IRE3–IRE9, IRE11, IRE12, IRE14). These results attest to the accuracy of the historical records of the 18th and 19th centuries' (with particular reference to Co. Donegal) and the natural population expansion in terms of distribution over the last 30 years and more from Co. Donegal into Co. Sligo (Carden et al., 2011). McDevitt et al. (2009a) showed varying levels of genetic diversity in Irish populations, and those with known, multiple introductions displayed higher levels of diversity (confirmed in this study also). The mean Irish diversity values are within the range of other European red deer populations (Appendix S6). Previous microsatellite analysis has also revealed gene flow between regions with known human-mediated translocations (McDevitt et al., 2009a). The results reported here provide further support for the mixed origins of these red deer populations within Ireland, which are the result of anthropogenic-mediated translocations of numbers of red deer between various Irish regions (McDevitt et al., 2009a), Scotland and England, as well as between Scotland, England, continental Europe and New Zealand (see Introduction). IRE1 was found in four Irish contemporary locations and Scotland (mainland and Rum), Cos Donegal, Galway, Sligo, one New Zealand sample and Co. Kerry, along with four ancient specimens dating to the Early Bronze Age–Iron Age (3340–2118 cal. yr BP; Cos Clare and Waterford: RD12, RD21, RD24, RD26; Appendix S2). The shared affinity between the Co. Kerry red deer with those from Co. Donegal can be explained by the documented historical translocations (see above), while those in Co. Galway can be explained due to the presence of a translocated herd of Killarney red deer to Connemara National Park in 1982 (source: National Parks and Wildlife Service, Ireland). County Wicklow haplotypes IRE13 and IRE14 haplotypes were associated with the Rum–Sardinia group. Apart from the translocation of unknown numbers of Scottish deer from the Island of Islay during the 1800s (Whitehead, 1960), there are no other documented introductions of this species to the east of Ireland. The Scottish island of Rum has a large proportion of Sardinian haplotypes so it is plausible that this haplogroup is also present on other Scottish islands due to translocations occurring within them. This could explain the presence of this haplogroup in Co. Wicklow. Haplotypes IRE9 and IRE10 were found in a particular stock of red deer found on the privately owned Screebe Estate (Co. Galway) in the west of Ireland. This particular herd was introduced to this region during the early 1980s and is derived from British park stock, namely Warnham Park, Sussex which is reflected in their close association with both English and European deer (Fig. 1b; Table 2).

The specimens dating to the Late Bronze Age–Iron Age (2954–1996 cal. yr BP; IRE15 – IRE18: RD03, RD05, RD17, RD22; Appendix S2) from the northwest (Co. Sligo), west (Co. Clare) and southeast (Co. Waterford) of Ireland were closely associated with haplotype IRE1 (all within a single bp; Fig. 1b). Interestingly, the final haplotype unique to Ireland (IRE2) was obtained not only from a fossil specimen dated to pre-LGM from a cave in Co. Waterford (RD23; Appendix S2), but also from a number of contemporary red deer from Co. Kerry, which was the less common of the two Co. Kerry haplotypes identified (Fig. 1b, Table 2). If the molecular data alone were examined, one could conclude from this result that the contemporary Co. Kerry population are descendants of red deer

that inhabited Ireland from before the LGM and therefore survived the Devensian Glaciation. Of the five supposed red deer dated pre-LGM specimens, three were identified via DNA as reindeer (*Rangifer* sp.). One specimen (a molar tooth) did not yield any genetic data, but it was re-checked by one of the authors (RFC) and, based on the morphology, determined positively as belonging to a red deer. In light of the identification of the reindeer specimens, the presence of red deer in Ireland pre-LGM may not have been substantial after all. There is then, along with other species, a significant absence of red deer radiocarbon dated records between *c* 29,500 cal. yr BP and *c* 13,300 cal. yr BP (Fig. 2). However, during the Late Glacial period, there are radiocarbon dated remains from giant deer, reindeer and red deer (Woodman et al., 1997), which re-colonised Ireland presumably from the nearest landmass which is now called Britain; these species could have swam across the Irish Sea (Stuart, 1995). In comparison, there are relatively more red deer radiocarbon dated material (and, therefore, more of an indicative presence of this species) from various sites in Britain during the Late Glacial (Yalden, 1999). It would seem, given no other evidence thus far to suggest otherwise, that the red deer in Ireland did not survive through the Late Pleistocene–Early Holocene transition, and this species became extirpated alongside the other two re-colonising deer species, during the Younger Dryas. Therefore, the shared haplotype between contemporary Co. Kerry individuals and that of the pre-LGM fossil could be the result of pre-LGM natural movement between Ireland and Britain (Martínková et al., 2007) and subsequent 're-stocking' of Ireland in the Neolithic period of a haplotype that is now no longer found in Britain (like the other Bronze and Iron Age haplotypes in Ireland; IRE15–IRE18: RD03, RD05, RD17, RD22). The TMRCA, based on the Co. Kerry red deer population, was estimated to 4901 cal. yr BP (95% CI 2447–8194 cal. yr BP) and is supportive of and compatible with the archaeological data with regards to the earliest presence of red deer skeletal remains during the Irish Neolithic period (Fig. 2, Appendix S5).

Although these molecular data shows a relationship between ancient Irish individuals, Co. Kerry and Scotland, there is a need to go further to rule out a more recent introduction in the last 200 years. In light of the results obtained from the genetic analyses and historical introductions, the craniometric analyses of the shape (and the size) of the female adult skulls indicated that the Scottish red deer were more similar to those from Co. Donegal (M3, M10, M19 and M36 measurements; data not shown), while both the Scotland and Co. Donegal deer were significantly different from the Co. Kerry deer. These findings are compatible with the molecular analyses and the historical records, where Co. Donegal red deer were introduced from amongst other locations, from Scottish herds, only 120 years ago (in 1891; see Introduction). Whereas, the introduction of red deer to Ireland (natural or deliberate) occurred at least 4000 years ago, thus allowing sufficient shape (and size) differences to evolve over time and separate the Co. Kerry population from the Co. Donegal and Scottish red deer populations.

The molecular and morphometric analyses point to the importance of the Neolithic period in the re-establishment of red deer in Ireland. During the Early Neolithic period, the first red deer remains, notably a worked antler (tine) fragment, is found associated with four human skeletons dated to *c* 5400 cal. yr BP from Annagh Cave, Co. Limerick (Ó Floinn, 2011a), although this date is inferred for the antler piece. With regards to actual red deer bone remains, the earliest dated material are from the Later Neolithic where numerous bones were found in the mudflats of the Fergus Estuary, Co. Clare (4874–4628 cal. yr BP, O'Sullivan, 2001; Appendix S2) and the remains of a near complete red deer stag which was found buried in a peat bog near Castlepollard, Co. Westmeath (4854–4531 cal. yr BP, Woodman et al., 1997; RD10, Appendix S2). Red deer skeletal remains account for less than 1% to

about 3% of faunal assemblages from a range of sites from the Neolithic to the Iron Age and much of this is represented by worked antler material (see Appendix S5). Although, it must be noted that the remains of red deer throughout much of the Neolithic period are represented in greater frequency by worked antler pieces rather than actual skeletal elements and, therefore, could either represent a small resident population or a population that was not hunted for its meat or other products; of the 25 possible Neolithic sites listed where red deer faunal material has been found, 16 of these contain worked antler fragments whereas only nine contain bone material (see Appendix S5). It is not until the Late Neolithic (4500 cal. yr BP), when the first relatively substantial finds of red deer skeletal remains are found from outside of the Newgrange Passage tomb in Co. Meath. However, of the full assemblage (12,000 bones) recovered, only 3% represent red deer (100 bones and antler fragments) (van Wijngaarden-Bakker, 1974, 1986). A similar pattern can be seen in the fauna from sites of Bronze Age and Early Iron Age dates. At Haughey's Fort (Co. Armagh) in an assemblage dating to 3000 cal. yr BP, six fragments of bone and antler were found in an assemblage of over 700 bones. At Dún Aillinne (Co. Kildare), a site that had continued use well into the Early Iron Age (i.e. close to 2000 cal. yr BP), red deer were represented by only three items out of an assemblage of over 2400 items. From the Bronze and Iron Ages (included radiocarbon dated specimens), we see relatively more frequent red deer skeletal elements, as opposed to just antler material, occurring, although they do not occur at any given site in large quantities in comparison to the domesticated species such as cattle, sheep and pig.

Red deer remains (bones, teeth and antler) were commonly found on many British Mesolithic and Neolithic sites, including some of the islands off Scotland (e.g. Morris, 2005; Mulville, 2010). In stark contrast, discounting the mis-identified and erroneous putative red deer remains from potentially Irish Mesolithic sites as well as those in later deposits (for example, Glenarm, Co. Antrim; Movius et al., 1937), there is a notable absence of red deer remains from the Irish Mesolithic (van Wijngaarden-Bakker, 1989; Woodman et al., 1997; McCormick, 1999; Woodman and McCarthy, 2003). Furthermore, when the distinctive lithic assemblage, characteristic of the human early colonisers (c 10,200 cal. yr BP; Woodman, 1978) found in the Irish Mesolithic period is considered in conjunction with a significant scarcity of scrapers and burins (used to modify antlers; Anderson, 1993; Woodman, 2000) and the absence of any antler material which was a vital raw material in tool manufacture, the presumed presence of red deer in the Irish Mesolithic period (Mitchell, 1956; Stuart, 1995) is unfounded.

The synthesis of results from this multi-disciplinary study involving archaeofaunal and historical data and records, radiocarbon dating, molecular and craniometric analyses all certainly indicate that red deer were either late colonisers (i.e. late natives; Searle, 2008) or were introduced by humans (i.e. early introductions; Searle, 2008) during the Irish Later Neolithic or Bronze Age periods. It is worth noting that a combination of fossil, morphological and genetic data has also been used to clarify the origin of red deer (C. e. corsicanus) on the Tyrrhenian islands Sardinia and Corsica, which, as a result, are believed to have been introduced to the islands during the Late Neolithic (Sardinia) and just before the beginning of Classical Antiquity (Corsica) (see Hajji et al., 2008 and references therein).

If red deer were deliberately introduced to Ireland by anthropogenic translocations from Britain then they may have been of both economic and social significance to the inhabitants (Soderberg, 2004; Morris, 2005). There is evidence, at least during the Neolithic, of social and material cultural connections between the northeast of Ireland and the southwest of Scotland and with the Isle of Man in the Irish Sea (pottery designs and megalithic tombs;

Sheridan, 2004; Cooney, 2004). Log boats and hide boats may have been widely used during the Neolithic, if not earlier (Vigne et al., 2009). However, aside from one fragment that might be part of a boat which was found at Woodend, Co. Tyrone (Fry, 2002), there are number of Neolithic dated boats; for example, the log boat from Lurgan, Addergoole, Co. Galway (Lanting and Brindley, 1996; Cooney, 2004). Livestock started to appear in Ireland during the Neolithic or possibly even earlier (Yalden, 1999; Woodman and McCarthy, 2003) — so why bring a wild ungulate? There is evidence of a special relationship between humans and red deer during prehistoric times. Deliberate early introductions of this species to areas devoid, or where there is little evidence of significant presence, of red deer suggest a special significance associated with ritual or economic reasons (Woodman and McCarthy, 2003), rather than the use of venison as a main food source (e.g. the Scottish islands; Sharples, 2000; Morris, 2005). Red deer remains, and more specifically antler tines or fragments thereof, were deposited in certain places during the Neolithic, Bronze Age, Iron Age and Early Medieval periods (e.g. Coffey et al., 1904; Hencken and Movius, 1934; Ó Floinn, 2011b). Additionally, the use of red deer frontlets has been associated with ritualistic functions, for example at Star Carr, a Mesolithic site in Britain (Legge and Rowley-Conwy, 1988).

5. Conclusions

Previous studies have highlighted a link between the Irish fauna and flora and those in southwestern Europe, both in terms of species assemblages (Corbet, 1961) and genetic affiliations (Searle, 2008). This was proposed to have occurred with early human traders, possibly Mesolithic. However, it is now becoming clear that this general model of species arriving in Ireland by similar means is too simplistic and unrealistic. This Neolithic link between Ireland and Britain that we have reported here for red deer has also recently been proposed to explain the accidental introduction of the pygmy shrew (Sorex minutus Linnaeus, 1766) to Ireland (McDevitt et al., 2011). Based on that study and the results reported here, it seems reasonable to assume that Ireland's nearest landmass (Britain) played a vital role in establishing its contemporary fauna and flora, and that Neolithic peoples likely transported these animals; accidentally in the case of the pygmy shrew and deliberately for the red deer. Therefore, it is clear that red deer were of significant cultural relevance to ancient peoples in Ireland. This long standing special human — red deer relationship is evident even in the present day. Considering its genetic and geographic isolation within Ireland (McDevitt et al., 2009a,b; Carden et al., 2011), the protection of Ireland's only ancient population of red deer, located in Killarney National Park and immediate surrounding lands should be a conservation priority and it should be given special significance within an Irish context.

Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quascirev.2012.02.012.

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