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Of mice and (Viking?) men: phylogeography of British and Irish house mice

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The west European subspecies of house mouse (*Mus musculus domesticus*) has gained much of its current widespread distribution through commensalism with humans. This means that the phylogeography of *M. m. domesticus* should reflect patterns of human movements. We studied restriction fragment length polymorphism (RFLP) and DNA sequence variations in mouse mitochondrial (mt) DNA throughout the British Isles (328 mice from 105 localities, including previously published data). There is a major mtDNA lineage revealed by both RFLP and sequence analyses, which is restricted to the northern and western peripheries of the British Isles, and also occurs in Norway. This distribution of the 'Orkney' lineage fits well with the sphere of influence of the Norwegian Vikings and was probably generated through inadvertent transport by them. To form viable populations, house mice would have required large human settlements such as the Norwegian Vikings founded. The other parts of the British Isles (essentially most of mainland Britain) are characterized by house mice with different mtDNA sequences, some of which are also found in Germany, and which probably reflect both Iron Age movements of people and mice and earlier development of large human settlements. MtDNA studies on house mice have the potential to reveal novel aspects of human history.

Keywords: colonization history; D-loop; mitochondrial DNA; *Mus musculus domesticus*; restriction fragment length polymorphisms; Vikings

1. INTRODUCTION

The colonization history of the house mouse *Mus musculus* is inextricably linked to human movements; large parts of its cosmopolitan range have been attained through passive transport by humans (Pocock *et al.* 2005). House mice can exploit the food of humans and their livestock, and are able to live in human dwellings, vehicles and boats. The western subspecies *Mus musculus domesticus*, in particular, was fortuitously placed, resident in the Fertile Crescent, at the time that humans first formed large settlements (8000 BC), and was able to become commensal with humans in such places (Brothwell 1981; Tchernov 1984). However, *M. m. domesticus* did not spread widely into Europe from the Middle East until the Iron Age (starting 1000 BC) (Cucchi *et al.* 2005). At this time, there was apparently extensive migration of the subspecies throughout the Mediterranean and western Europe.

This link between humans and house mice is noteworthy. It means that the colonization history of house mice should reflect human migrations and trading links, and even colonization events. Therefore, a knowledge of the colonization history of this commensal may be a valuable archaeological tool, revealing events in human history that are not well represented in artefacts or written documents (Gündüz *et al.* 2001; Haynes *et al.* 2003).

A powerful way to infer the colonization history of a species is through phylogenetic studies of molecular markers in a geographical context. This 'phylogeographic' approach (Avise 2000) has been used with much effect, e.g. in tracing the postglacial colonization history of European fauna and flora (Hewitt 2000). Mitochondrial (mt) DNA has been the best-studied genomic region in the phylogeographic studies of mammals, and in the house mouse there have already been extensive studies, particularly by Prager and colleagues on complete D-loop sequences (Prager *et al.* 1993, 1996, 1998; see also

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Gündüz *et al.* 2005; Ihle *et al.* 2006; Rajabi-Maham *et al.* 2008). As regards *M. m. domesticus*, there is substantial D-loop variation and little geographical structure throughout much of the Mediterranean and the nearby areas of western Europe. These and similar findings with allozymes (Britton-Davidian 1990) suggest that when colonization of these areas did occur, it involved rapid mass migration rather than some protracted stepping stone process, which is very much in line with the archaeological findings. However, following earlier restriction fragment length polymorphism (RFLP) analysis (Ferris *et al.* 1983; Gyllensten & Wilson 1987), D-loop sequencing of house mice in Scandinavia showed a much more surprising result: that Sweden and northern Denmark were colonized by house mice following a founder event, with the colonists characterized by the mtDNA of *M. m. domesticus*, but the nuclear DNA of the eastern subspecies *M. m. musculus* (Prager *et al.* 1993). Remarkably, the same *M. m. domesticus* mtDNA haplotypes that characterized the house mice colonizing Scandinavia are also found in Madeira, prompting suggestions that Danish Vikings took mice to Madeira long before the official discovery of the island by the Portuguese (Gündüz *et al.* 2001). Comparisons of nuclear and mitochondrial data for these Madeiran mice support the contention that mtDNA is a particularly good marker for the source of the first colonization of a particular area by mice (Britton-Davidian *et al.* 2007).

Given that the phylogeography of house mice around the Atlantic periphery of Europe has yielded such interesting results, it is worthwhile to examine the colonization history of the British Isles by *M. m. domesticus*. The British Isles have had a complex human history over the last 3000 years including participation by both Danish and Norwegian Vikings. In Britain, the earliest records of house mice date from the Bronze Age (figure 1); though given the finding elsewhere in western Europe that the species did not arrive until the Iron Age, these early records may not be secure (e.g. they could be intrusive). In general, the Iron Age records of house mice come from southern Britain, while there is a substantial amount of Roman material from central Britain. There are no records of house mice from Ireland contemporary with the British Bronze Age, Iron Age or Roman periods.

For the phylogeographic study of the house mouse in the British Isles reported here, we incorporate all relevant mtDNA data available. This includes published mt D-loop sequences as well as our previously unreported RFLP and sequence data collected over the last 20 years. Together, these provide a good coverage of the British Isles, including a particularly detailed representation of Orkney and the neighbouring part of mainland Britain.

2. MATERIAL AND METHODS

(a) *Specimens*

Using molecular techniques, we typed 310 mice from 96 localities in the British Isles (appendices 2 and 3 in the electronic supplementary material), adding to published data for 18 individuals (nine additional localities). The mice that we typed were either collected by ourselves, generally through live trapping on farms, or provided by colleagues, as listed in appendix 2. Whole specimens or tissue samples were stored frozen (−80°C) or in absolute ethanol.

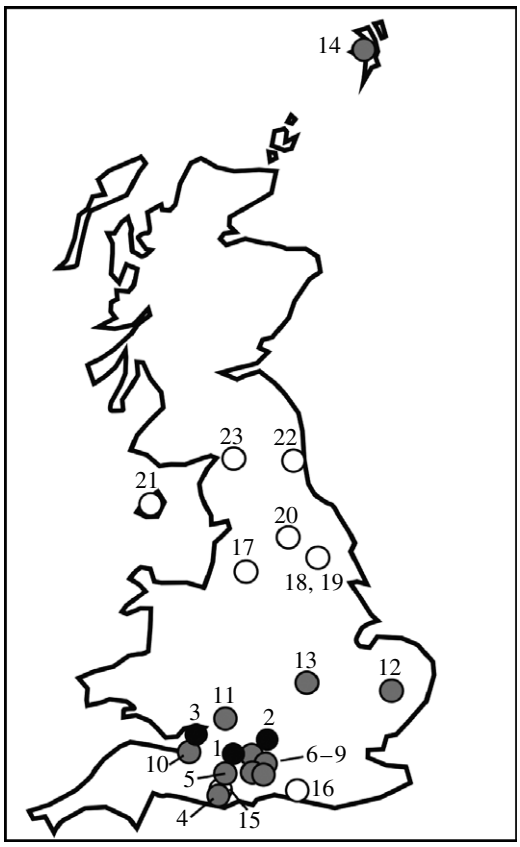

Figure 1. Archaeological records of house mice in Britain (see appendix 1 in the electronic supplementary material for further details). Following the chronology by the British and Irish Archaeological Bibliography (http://www.biab.ac.uk/chronology.asp), Bronze Age (black circles) is considered as 2300–700 BC, Iron Age (grey circles; lowland Britain) as 700 BC to AD 43 and Roman (white circles; lowland Britain) as AD 43–450. As most records are from lowland Britain, we retain the chronological framework from lowland Britain when referring to sites elsewhere.

(b) *Molecular methods and analysis*

For RFLP analysis, mitochondria were prepared from heart and kidneys using differential centrifugation procedures and mtDNA isolated by a modified phenol extraction procedure (Jones *et al.* 1988). DNA samples were digested with 13 restriction enzymes (appendix 4 in the electronic supplementary material). Fragments were separated either on 5 per cent polyacrylamide gels run for 3 hours and visualized by silver staining (Tegelström 1986), or run on 0.8 per cent agarose gels in TBE (89 mM Tris–HCl, 89 mM boric acid, 2 mM EDTA (pH 8.0)), and stained with ethidium bromide. The sizes of the fragments were estimated by comparing them with the fragments of known sizes from the published mouse mtDNA sequence (Bibb *et al.* 1981), run as a standard on each gel and cut with the appropriate enzyme.

Each restriction fragment digestion profile was site mapped using the sequence comparison method (Cann *et al.* 1982), in which restriction sites required to account for each fragment pattern were determined by reference to Bibb *et al.* (1981) and the existing maps (Ferris *et al.* 1983; Sage *et al.* 1990). A composite genotype was thus generated for each individual based on the presence and absence of each restriction site. These genotypes were incorporated into a data matrix used in an undirected parsimony analysis with PAUP* v. 4.0 (Swofford 2002), generating a 50 per cent majority-rule consensus tree after

a 1000 replicates of a heuristic search with random stepwise addition of taxa. Nodal support was estimated by bootstrap resampling ($n=1000$).

For DNA sequencing of all or part of the mitochondrial D-loop, total genomic DNA was extracted from tissue samples (normally tail tip) by phenol–chloroform or with Qiagen DNeasy tissue kits. The complete mt D-loop and flanking regions were amplified with the PCR primers and the conditions as described by Gündüz *et al.* (2000), or with the primer pairs L831-5′-ATACGCCATTCTACGCTCAA-3′ and H2228-5′-TTATAAGGCCAGGACCAAAC-3′. The fragments generated were sequenced in both directions using the same primers. The sequences were aligned and edited using SEQUENCHER v. 4.8 (Gene Codes Corp.). For all specimens, we obtained sequences for the mtDNA region between positions 15 363 and 16 295 (933 bp) of Bibb *et al.* (1981). These were then truncated to a standard length of 853 bp, between positions 15 424 and 16 276, for comparison with other sequences. Our sequences have been deposited in GenBank (FM211596–FM211631).

All the complete D-loop sequences from the British Isles were combined with every equivalent published *M. m. domesticus* sequence, including those in the companion paper (Searle *et al.* in press), for phylogenetic analysis. GenBank sequences of the following were used as outgroups, adopting Rajabi-Maham *et al.* (2008): *M. m. gentilulus*, AF074545 and AF074544; *M. m. castaneus*, EF108342, AF088879 and AJ286322; and *M. m. musculus*, U47504 and U47532. The GTR+I+Γ substitution model was selected using MODELTEST v. 3.7 (Posada & Crandall 1998). Also following Rajabi-Maham *et al.* (2008), we employed a Bayesian algorithm to analyse our data, using the program MRBAYES (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) to construct a 50 per cent majority-rule consensus tree. Two independent Markov chain Monte Carlo analyses were run, each with one cold chain and four heated chains and the incremental heating parameter set at 0.2. The analyses were terminated after 5 million generations and the first 30 per cent of trees were discarded as burn-in.

For some populations, partial D-loop sequences were obtained as a preliminary to selective complete D-loop sequencing (Gündüz 1999). Partial D-loop sequences were generated with primers L15774 and H16498 using the conditions described in Gündüz *et al.* (2000). This produced a 305 bp sequence between positions 15 363 and 15 667 of Bibb *et al.* (1981) including the left end of the D-loop (251 bp) and part of the Pro-tRNA (54 bp). Despite the short length of the sequence, partial D-loop sequences capture the majority of nucleotide variation displayed by complete D-loop sequences (see appendix 5 in the electronic supplementary material). Therefore, the partial sequences could be allocated with ease into the major lineages identified by the analysis of the complete D-loop sequences.

Nucleotide (π) and haplotype (h) diversities for the D-loop sequences were calculated according to Nei (1987), using MEGA v. 4 (Tamura *et al.* 2007) and ARLEQUIN v. 3.0 (Excoffier *et al.* 2005), respectively. These diversities were estimated on an unbiased dataset of complete D-loop sequences collected from throughout the British Isles (80 individuals). Our new complete D-loop sequences from localities 20–25, 27–29, 37, 38 and 47 were excluded from the analysis owing to the bias introduced by selecting individuals for complete sequencing on the basis of their partial sequence.

3. RESULTS

New complete D-loop sequences were generated from 77 house mice from the British Isles adding to 18 published sequences (11 haplotypes). Altogether, the 95 mice are represented by 40 haplotypes (appendices 2 and 5 in the electronic supplementary material). The overall haplotype ($h\pm$s.d.) and nucleotide diversities ($\pi\pm$s.d.) are 0.955 ± 0.009 and 0.0069 ± 0.0017, respectively. Seven haplotypes were found in five or more individuals within the British Isles. BritIsl.8, 19 and 26 were restricted to the Scottish archipelagos of Shetland, Orkney and the Outer Hebrides, respectively. BritIsl.1, 5, 16 and 31 were wide ranging in the British Isles, and also have been found elsewhere in the world (appendix 6 in the electronic supplementary material). BritIsl.1 was found in northern Scotland (Sutherland), southern Scotland (Dumfries), northern England (York), southern England (e.g. Wiltshire) and the Isle of Man. It has also been found in Germany, New Zealand and Mauritania. BritIsl.5 was found in southern Scotland (East Lothian), southern England (e.g. Somerset), Islay (Scotland) and Anglesey (Wales), and has also been found in Germany, Denmark, Norway, New Zealand and Cameroon; BritIsl.16 was found in Orkney, Ireland and Norway; and BritIsl.31 was found in Orkney, northern Scotland (e.g. Caithness), Ireland, Norway and Portugal. There are two additional haplotypes known from both the British Isles and elsewhere in the world: BritIsl.12 (Germany) and BritIsl.14 (Portugal).

When combined with all other available D-loop sequences of *M. m. domesticus* in a Bayesian analysis, most of the haplotypes, including all those found to be widely distributed in the British Isles, form two major lineages (figure 2 and appendix 6 in the electronic supplementary material): one which includes BritIsl. 1–10 is well supported (posterior probability 0.96) and the other (which includes BritIsl.16–36) is poorly supported (posterior probability 0.65), which is typical of other lineages that have been identified in *M. m. domesticus* phylogenetic trees (Prager *et al.* 1993, 1996, 1998; Gündüz *et al.* 2001, 2005; Rajabi-Maham *et al.* 2008), due to the recent diversification and high levels of homoplasy associated with the highly variable D-loop region (Rajabi-Maham *et al.* 2008). The remaining haplotypes (BritIsl.11–15) are located elsewhere in the phylogenetic tree (figure 2).

The lineage consisting of haplotypes BritIsl.16–36 has occurred as a separate lineage in all previous phylogenetic analyses that have included the relevant haplotypes (Prager *et al.* 1993, 1996, 1998; Nachman *et al.* 1994; Gündüz *et al.* 2001, 2005). The lineage has a striking distribution in the British Isles relative to other *M. m. domesticus* haplotypes (appendix 2 in the electronic supplementary material). It is restricted to the northern and western peripheries (the Outer Hebrides, Shetland and Orkney and nearby mainland, and Ireland). Because its association has been demonstrated particularly clearly with Orkney, we term this the 'Orkney' mtDNA lineage. *Mus musculus domesticus* with haplotypes distinct from this Orkney lineage have been found throughout mainland Britain and in parts of Ireland, the Isle of Man and Shetland.

Further confirmation of the geographical range of the Orkney mtDNA lineage comes from partial D-loop

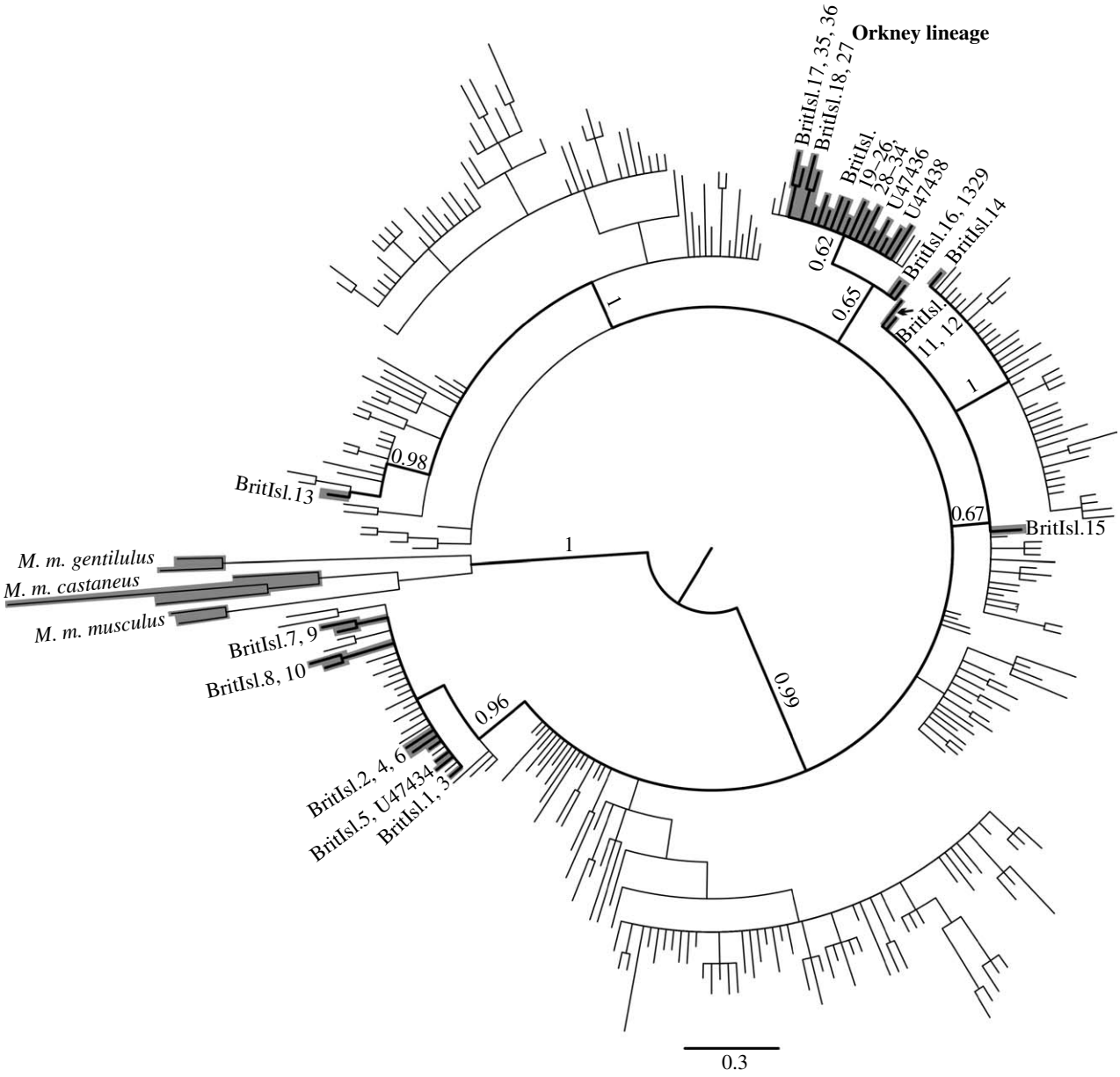

Figure 2. Phylogenetic tree for *M. m. domesticus* from complete mtDNA D-loop sequences after Bayesian analysis (see text). The tree shows all house mouse haplotypes found in the British Isles together with all available haplotypes from GenBank. All posterior probabilities of 0.60 or greater are shown for branches leading to British haplotypes.

sequences and RFLP data of the entire mtDNA genome (appendices 2 and 4 in the electronic supplementary material). Again, in the phylogenetic tree generated from the RFLP data, the Orkney lineage appears as a clear entity clustering together individuals from Orkney and its vicinity, the Isle of Man, and Ireland to the exclusion of individuals from England, Wales and southern Scotland. Altogether, there are substantial data to show that Orkney and the nearby mainland (Caithness) are occupied almost solely by the mice of the Orkney mtDNA lineage, which is also predominant in the western parts of the British Isles (figure 3).

4. DISCUSSION

The spread of *M. m. domesticus* throughout much of the world began with populations in the Middle East that first associated with humans *ca* 8000 BC (Cucchi *et al.* 2005). The British Isles are clearly at the periphery of the western European expansion of this house mouse subspecies, despite which there is substantial genetic variation here, as reflected, for instance, by comparison of haplotype and nucleotide diversities with Turkey (British Isles: $h=0.96$, $\pi=0.0069$; Turkey: $h=0.98$, $\pi=0.0084$; Gündüz *et al.* 2005; see also Rajabi-Maham *et al.* 2008). However, while the variation shows only weak geographical structure in Turkey (Gündüz *et al.* 2005), it is strongly regionalized in the British Isles. In particular, there is an Orkney mtDNA lineage that is predominant in and restricted to the northern and western peripheries of the British Isles (Orkney, Shetland, Outer Hebrides, Isle of Man, Ireland; figure 3). Given that house mice mtDNA haplotypes are a marker of human movements, it is pertinent to consider how this has come about. It is especially striking that the Orkney mtDNA lineage has a distribution within the British Isles that matches the Norwegian Viking sphere of influence (Logan 1991). Accordingly, the name of the lineage is apposite: Orkney was a key centre within the Norwegian Viking kingdom in the eleventh and twelfth centuries AD (Crawford 1987; Forte *et al.* 2005).

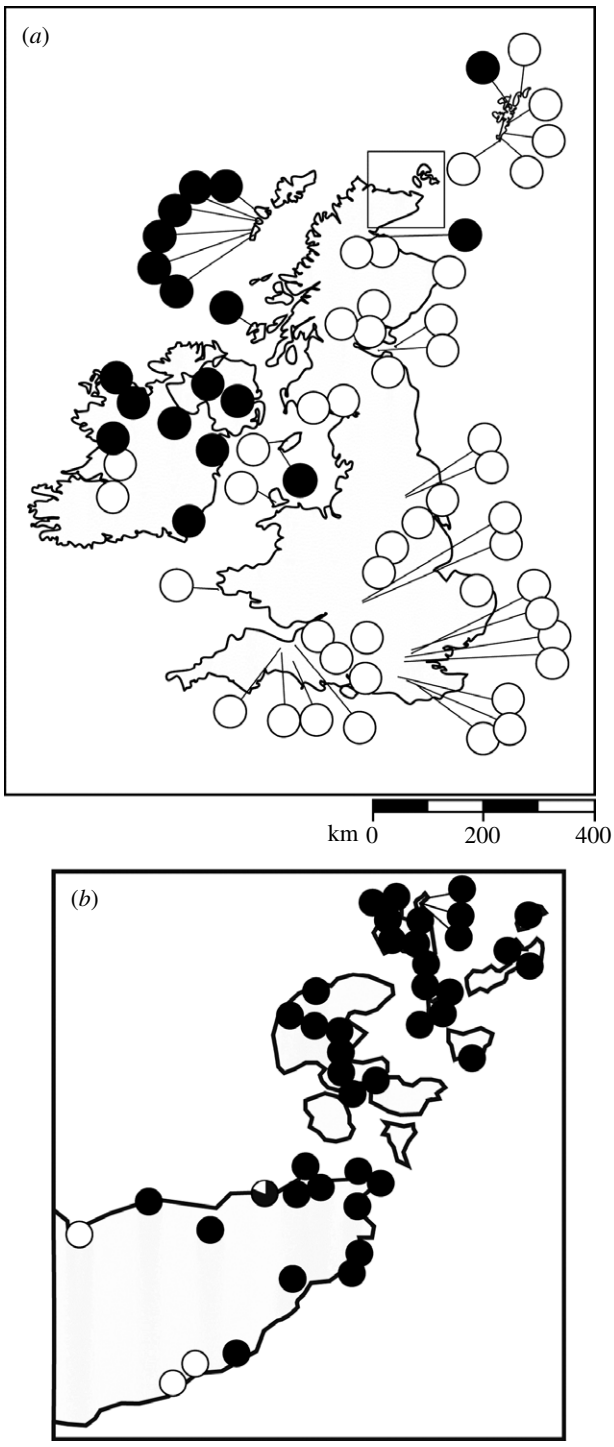

Figure 3. The distribution of haplotypes of the Orkney mtDNA lineage (black circles) and other haplotypes (white circles) among 328 house mice from 105 localities distributed over the (*a*) British Isles and (*b*) Orkney and the nearby British mainland. Each pie represents a single collection locality with black circles indicating the proportion of individuals of the Orkney mtDNA lineage. Data taken from complete and partial mtDNA D-loop sequences, and RFLP data from the complete mtDNA genome.

Further support for a causal linkage between the Orkney lineage and Norwegian Vikings comes from the available mtDNA sequences from Norway, both published and previously unreported (see appendices 2 and 6 in the electronic supplementary material). Eight out of nine mice sampled from two locations on the coast of central Norway were of the Orkney lineage (four haplotypes). Furthermore, two of those Orkney haplotypes found in Norway (BritIsl.16 and 31) have a wide distribution around the area occupied by the Norwegian Vikings (including Orkney, Ireland and Norway), suggesting that the sphere of influence is reflected not just by a lineage but by specific haplotypes. Such haplotypes are likely to have been some of those present at the time of the transport of the house mice; other haplotypes in the lineage may have evolved *in situ* through mutation.

There is also evidence of distinctiveness of the Orkney, Shetland and Caithness populations of house mice relative to the rest of the British mainland on the basis of morphometrics, allozyme variation and Y chromosome DNA variation (Berry & Peters 1977; Davis 1983; Nash *et al.* 1983; Jones 1990).

How can the association of the Orkney lineage and Norwegian Vikings be explained? Clearly, house mice were present in Britain long before the first visits to the British Isles by Norwegian Vikings in AD 793 (Logan 1991). Both the analysis of spread of *M. m. domesticus* in the Mediterranean region (Cucchi *et al.* 2005) and the archaeological records within Britain (figure 1) are consistent with the arrival of house mice in Britain in the Iron Age, i.e. at least 2 kyr ago. Therefore, it is to be expected that at least some of the house mice in the British Isles would have a genetic architecture that reflects pre-Viking origins, and this is indeed seen. The first settlements of any size in Britain are suggested to be Iron Age hill forts in southern England (Collis 1984; Bewley 1994; Cunliffe 2004), while it is with the arrival of the Romans that towns (albeit garrison towns) emerge further north (Harding 2004). This pattern is reflected by the earliest archaeological records of house mice (figure 1), which fits with the dependence of house mice on large settlements for long-term persistence (Cucchi *et al.* 2005). Only in large human settlements are house mice able to form viable populations when in competition with the wood mouse *Apodemus sylvaticus* (Cucchi *et al.* 2005), a species that occurs throughout the British Isles. Apparently, house mice of the mtDNA lineage including BritIsl.1–10 especially exploited these early large settlements and ultimately expanded over most of mainland Britain. Two haplotypes of this lineage are distributed particularly widely in Britain (BritIsl.1 and 5) and are also found in Germany. There were substantial human cultural contacts between middle and northern Europe and Britain in the Iron Age (Cunliffe 2004), and it can be proposed that ancestors of these mice came from Germany at that time.

Considering now the northern and western peripheries of the British Isles currently occupied by the Orkney lineage, there is limited evidence for a pre-Viking presence of house mice in this area. There is a script from Ireland dating to the seventh century AD that refers to house mice (Hayden 2002), but such anecdotal records are contentious owing to the possibility of confusion between house and wood mice. An archaeological investigation by Nicholson *et al.* (2005) recorded a single house mouse from an apparently secure Iron Age deposit on Shetland, but even such a record needs confirmation with carbon dating of the bones. The lack of records of house mice from pre-Viking archaeological sites on Orkney is telling, because small mammal bones are particularly well represented and studied there (Nicholson *et al.* 2005).

Whether or not there were occasional pre-Viking house mice in the region now occupied by the Orkney lineage, more important in terms of the current genetic signal would have been the development of large sustained mouse populations associated with the founding of substantial human settlements. For much of the area covered by the Orkney lineage, the Viking era is the time when urban settlements were initiated, particularly so for Ireland. Prior to the Viking era, there were no towns or large settlements in Ireland (Delany 1977); during the Viking period, the first towns were founded at Limerick, Waterford, Wicklow, Wexford, Dublin and near Cork and Lough (Logan 1991; Forte *et al.* 2005).

It is our contention, therefore, that for the house mouse the Orkney mtDNA lineage represents a marker for Norwegian Viking influence. It should not be assumed, however, that mice with the Orkney lineage originated in Norway and were taken to the British Isles. The transport may have been in the other direction, but still made by Norwegian Vikings. Our results add to the previously described association between Madeiran mice and Danish Vikings (Gündüz *et al.* 2001), in indicating that house mice are a valuable proxy for Viking movements, as revealed through the studies of mtDNA. The combination in the Viking period of the spread of urbanization in northwestern Europe and the trade facilitated by sophisticated ships capable of travelling substantial distances and carrying large amounts of cargo make the Vikings ideal house mouse vectors. There is clear evidence from Viking-age deposits in Iceland and Greenland that house mice were indeed transported on Viking ships (Nicholson *et al.* 2005).

An obvious use of the Orkney mouse lineage as a marker for the Norwegian Vikings is that we may be able to help confirm their activities outside the British Isles. Fine-scale genetic analysis of house mice has the potential to reveal precise cultural associations within the former Norwegian Viking kingdom including Faroe, Iceland, Greenland and Newfoundland. We are currently conducting research in these directions (E. P. Jones & J. B. Searle 2008, unpublished data).

The mtDNA variation of house mice in the British Isles is not only relevant to movements of people and their commensals during the Iron Age and Viking times. The occurrence of house mice with British haplotypes in New Zealand is described in the companion paper (Searle *et al.* in press), and reflects much more recent human movements, in this case from Britain to New Zealand. The clustering of BritIsl.13 with haplotypes from the USA (appendix 6 in electronic supplementary material) may reflect a lineage that colonized North America from Britain.

Thus, on the time scale of the last 3000 years, it is evident that house mice mirror well the movements of human beings, and therefore the study of their phylogeography represents an unusual, underused, but valuable, aid to archaeologists and historians. Here, we have analysed mtDNA variation to useful effect. In the future, there is clearly the exciting opportunity to extend the phylogeographic analysis radically to exploit the nuclear genome resources of the house mouse (Mouse Genome Sequencing Consortium 2002).

We are extremely grateful for all those who provided the specimens used in this analysis (listed in appendix 2 in the electronic supplementary material), including Graham Triggs and Marcus Hewson for their assistance with some island fieldwork. We also thank Keith Dobney for help with archaeological records, Matthew King for aid with the maps, and the editor and referees for their comments on the paper. Funding was provided by the University of York, the Biotechnology and Biological Sciences Research Council (advanced fellowship to C.S.J., 1/AF09056), the Scientific and Technological Research Council of Turkey (TÜBİTAK), the Skye Foundation and the South African National Research Foundation and Programme Alβan (EU). Part of this work was carried out by using the resources of the Computational Biology Service Unit from the Cornell University, which is partially funded by Microsoft Corporation.

REFERENCES

Avise, J. C. 2000 *Phylogeography: the history and formation of species*. Cambridge, MA: Harvard University Press.

Berry, R. J. & Peters, J. 1977 Heterogeneous heterozygosities in *Mus musculus* populations. *Proc. R. Soc. B* **197**, 485–503. (doi:10.1098/rspb.1977.0082)

Bewley, R. H. 1994 *Prehistoric settlements*. London, UK: Batsford.

Bibb, M. J., Van Etten, R. A., Wright, C. T., Walberg, M. W. & Clayton, D. A. 1981 Sequence and gene organization of mouse mitochondrial DNA. *Cell* **26**, 167–180. (doi:10.1016/0092-8674(81)90300-7)

Britton-Davidian, J. 1990 Genic differentiation in *M. m. domesticus* populations from Europe, the Middle East and North Africa: geographic patterns and colonization events. *Biol. J. Linn. Soc.* **41**, 27–45. (doi:10.1111/j.1095-8312.1990.tb00819.x)

Britton-Davidian, J., Catalan, J., Lopez, J., Ganem, G., Nunes, A. C., Ramalhinho, M. G., Auffray, J. C., Searle, J. B. & Mathias, M. L. 2007 Patterns of genic diversity and structure in a species undergoing rapid chromosomal radiation: an allozyme analysis of house mice from the Madeira archipelago. *Heredity* **99**, 432–442. (doi:10.1038/sj.hdy.6801021)

Brothwell, D. 1981 The Pleistocene and Holocene archaeology of the house mouse and related species. *Symp. Zool. Soc. Lond.* **47**, 1–13.

Cann, R. L., Brown, W. H. & Wilson, A. C. 1982 Evolution of human mitochondrial DNA: a preliminary report. In *Human genetics, part A: the unfolding genome* (eds B. Bonne-Tamir, P. Cohen & R. N. Goodman), pp. 157–165. New York, NY: Alan Liss.

Collis, J. R. 1984 *The European Iron Age*. London, UK: Routledge.

Crawford, B. E. 1987 *Scandinavian Scotland*. Leicester, UK: Leicester University Press.

Cucchi, T., Vigne, J.-D. & Auffray, J.-C. 2005 First occurrence of the house mouse (*Mus musculus domesticus* Schwarz and Schwarz, 1943) in the Western Mediterranean: a zooarchaeological revision of subfossil house mouse occurrences. *Biol. J. Linn. Soc.* **84**, 429–445. (doi:10.1111/j.1095-8312.2005.00445.x)

Cunliffe, B. W. 2004 *Iron Age communities in Britain: an account of England, Scotland and Wales from the seventh century BC until the Roman conquest*, 4th edn. London, UK: Routledge.

Davis, S. J. M. 1983 Morphometric variation of populations of house mice *Mus domesticus* in Britain and Faroe. *J. Zool.* **199**, 521–534.

Delany, T. G. 1977 The archaeology of the Irish town. In *European towns: their archaeology and early history* (ed. M. W. Barley), pp. 47–64. London, UK: Academic Press.

Excoffier, L., Laval, G. & Schneider, S. 2005 ARLEQUIN. 3.0 an integrated software package for population genetics data analysis. *Evol. Bioinform. Online* **1**, 47–50.

Ferris, S. D., Sage, R. D., Huang, C.-M., Nielsen, J. T., Ritte, U. & Wilson, A. C. 1983 Flow of mitochondrial DNA across a species boundary. *Proc. Natl Acad. Sci. USA* **80**, 2290–2294. (doi:10.1073/pnas.80.8.2290)

Forte, A., Oram, R. & Pedersen, F. 2005 *Viking empires*. Cambridge, UK: Cambridge University Press.

Gündüz, İ. 1999 Evolutionary genetics of the house mouse (*Mus musculus domesticus*) with particular emphasis on chromosomal and mitochondrial DNA variation. DPhil thesis, University of York.

Gündüz, İ., Tez, C., Malikov, V., Vaziri, A., Polyakov, A. V. & Searle, J. B. 2000 Mitochondrial DNA and chromosomal studies of wild mice (*Mus*) from Turkey and Iran. *Heredity* **84**, 458–467. (doi:10.1046/j.1365-2540.2000.00694.x)

Gündüz, İ., Auffray, J.-C., Britton-Davidian, J., Catalan, J., Ganem, G., Ramalhinho, M. G., Mathias, M. L. & Searle, J. B. 2001 Molecular studies on the colonization of the Madeiran archipelago by house mice. *Mol. Ecol.* **10**, 2023–2029. (doi:10.1046/j.0962-1083.2001.01346.x)

Gündüz, İ., Rambau, R. V., Tez, C. & Searle, J. B. 2005 Mitochondrial DNA variation in the western house mouse (*Mus musculus domesticus*) close to its site of origin: studies in Turkey. *Biol. J. Linn. Soc.* **84**, 473–485. (doi:10.1111/j.1095-8312.2005.00448.x)

Gyllensten, U. & Wilson, A. C. 1987 Interspecific mitochondrial DNA transfer and the colonization of Scandinavia by mice. *Genet. Res.* **49**, 25–29.

Harding, D. W. 2004 *The Iron Age in northern Britain: Celts and Romans, natives and invaders*. London, UK: Routledge.

Hayden, T. J. 2002 The assembly of Ireland's freshwater fish, amphibia, reptiles and mammals: tempo and mode. In *Biological invaders: the impact of exotic species* (eds C. Moriarty & D. Murray), pp. 15–29. Dublin, Ireland: Royal Irish Academy.

Haynes, S., Jaarola, M. & Searle, J. B. 2003 Phylogeography of the common vole (*Microtus arvalis*) with particular emphasis on the colonization of the Orkney archipelago. *Mol. Ecol.* **12**, 951–956. (doi:10.1046/j.1365-294X.2003.01795.x)

Hewitt, G. 2000 The genetic legacy of the Quaternary ice ages. *Nature* **405**, 907–913. (doi:10.1038/35016000)

Huelsenbeck, J. P. & Ronquist, F. 2001 MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755. (doi:10.1093/bioinformatics/17.8.754)

Ihle, S., Ravaoarimanana, I., Thomas, M. & Tautz, D. 2006 An analysis of signatures of selective sweeps in natural populations of the house mouse. *Mol. Biol. Evol.* **23**, 790–797. (doi:10.1093/molbev/msj096)

Jones, C. S. 1990 Mitochondrial DNA variation in British house mice (*Mus domesticus*, Rutty). PhD thesis, University of London.

Jones, C. S., Tegelström, H., Latchman, D. & Berry, R. J. 1988 An improved rapid method for mitochondrial isolation suitable for use in the study of closely related populations. *Biochem. Genet.* **26**, 83–88. (doi:10.1007/BF00555490)

Logan, F. D. 1991 *The Vikings in history*, 2nd edn. London, UK: Routledge.

Mouse Genome Sequencing Consortium 2002 Initial sequencing and comparative analysis of the mouse genome. *Nature* **420**, 520–562. (doi:10.1038/nature01262)

Nachman, M. W., Boyer, S. N., Searle, J. B. & Aquadro, C. F. 1994 Mitochondrial DNA variation and the evolution of Robertsonian chromosomal races of house mice, *Mus domesticus*. *Genetics* **136**, 1105–1120.

Nash, H. R., Brooker, P. C. & Davis, S. J. M. 1983 The Robertsonian translocation house-mouse populations of North East Scotland: a study of their origin and evolution. *Heredity* **50**, 303–310. (doi:10.1038/hdy.1983.32)

Nei, M. 1987 *Molecular evolutionary genetics*. New York, NY: Colombia University Press.

Nicholson, R. A., Barber, P. & Bond, J. M. 2005 New evidence for the date of introduction of the house mouse, *Mus musculus domesticus* Schwartz & Schwartz, and the field mouse, *Apodemus sylvaticus* (L.), to Shetland. *Environ. Archaeol.* **10**, 143–151.

Pocock, M. J. O., Hauffe, H. C. & Searle, J. B. 2005 Dispersal in house mice. *Biol. J. Linn. Soc.* **84**, 565–583. (doi:10.1111/j.1095-8312.2005.00455.x)

Posada, D. & Crandall, K. A. 1998 MODELTEST: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. (doi:10.1093/bioinformatics/14.9.817)

Prager, E. M., Sage, R. D., Gyllensten, U., Thomas, W. K., Hübner, R., Jones, C. S., Noble, L., Searle, J. B. & Wilson, A. C. 1993 Mitochondrial DNA sequence diversity and the colonization of Scandinavia by house mice from East Holstein. *Biol. J. Linn. Soc.* **50**, 85–122. (doi:10.1111/j.1095-8312.1993.tb00920.x)

Prager, E. M., Tichy, H. & Sage, R. D. 1996 Mitochondrial DNA sequence variation in the eastern house mouse, *Mus musculus*: comparison with other house mice and report of a 75-bp tandem repeat. *Genetics* **143**, 427–446.

Prager, E. M., Orrego, C. & Sage, R. D. 1998 Genetic variation and phylogeography of central Asian and other house mice, including a major new mitochondrial lineage in Yemen. *Genetics* **150**, 835–861.

Rajabi-Maham, H., Orth, A. & Bonhomme, F. 2008 Phylogeography and postglacial expansion of *Mus musculus domesticus* inferred from mitochondrial DNA coalescent, from Iran to Europe. *Mol. Ecol.* **17**, 627–641. (doi:10.1111/j.1365-294X.2007.03601.x)

Ronquist, F. & Huelsenbeck, J. P. 2003 MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574. (doi:10.1093/bioinformatics/btg180)

Sage, R. D., Prager, E. M., Tichy, H. & Wilson, A. C. 1990 Mitochondrial DNA variation in house mice, *Mus domesticus* (Rutty). *Biol. J. Linn. Soc.* **41**, 105–123. (doi:10.1111/j.1095-8312.1990.tb00824.x)

Searle, J. B., Jamieson, P. M., Gündüz, İ., Stevens, M. I., Jones, E. P., Gemmill, C. E. C. & King, C. M. In press. The diverse origins of New Zealand house mice. *Proc. R. Soc B.* (doi:10.1098/rspb.2008.0959)

Swofford, D. L. 2002 *PAUP*. Phylogenetic analysis using parsimony (* and other methods). v. 4.0 beta*. Sunderland, MA: Sinauer Associates.

Tamura, K., Dudley, J., Nei, M. & Kumar, S. 2007 MEGA4: molecular evolutionary genetics analysis (MEGA) software v. 4.0. *Mol. Biol. Evol.* **24**, 1596–1599. (doi:10.1093/molbev/msm092)

Tchernov, E. 1984 Commensal animals and human sedentism in the Middle East. In *Animals and archaeology: 3. Early herders and their flocks* (eds J. Clutton-Brock & G. Grigson), pp. 91–115. Oxford, UK: British Archaeological Reports, International Series.

Tegelström, H. 1986 Mitochondrial DNA in natural populations: an improved routine for the screening of genetic variation based on sensitive silver staining. *Electrophoresis* **7**, 226–229. (doi:10.1002/elps.1150070508)