The diverse origins of New Zealand house mice

Jeremy B. Searle^{1,*†}, Paul M. Jamieson^{2,†}, İslam Gündüz^{1,3,†},
Mark I. Stevens^{4,5,†}, Eleanor P. Jones¹, Chrissen E. C. Gemmill²
and Carolyn M. King^{2,†}

¹Department of Biology (Area 2), University of York, PO Box 373, York YO10 5YW, UK

²Centre for Biodiversity and Ecology Research, Department of Biological Sciences, University of Waikato,
Hamilton 3240, New Zealand

³Department of Biology, Faculty of Arts and Sciences, University of Ondokuz Mayıs, Samsun 55139, Turkey

⁴Allan Wilson Centre for Molecular Ecology and Evolution, Massey University, Palmerston North 5320, New Zealand

⁵South Australian Museum, SA 5000, and School of Biological Sciences, Flinders University, SA 5001, Adelaide, Australia

Molecular markers and morphological characters can help infer the colonization history of organisms. A combination of mitochondrial (mt) D-loop DNA sequences, nuclear DNA data, external measurements and skull characteristics shows that house mice (*Mus musculus*) in New Zealand and its outlying islands are descended from very diverse sources. The predominant genome is *Mus musculus domesticus* (from western Europe), but *Mus musculus musculus* (from central Europe) and *Mus musculus castaneus* (from southern Asia) are also represented genetically. These subspecies have hybridized to produce combinations of *musculus* and *domesticus* nuclear DNA coupled with *domesticus* mtDNA, and *castaneus* or *musculus* mtDNA with *domesticus* nuclear DNA. The majority of the mice with *domesticus* mtDNA that we sampled had D-loop sequences identical to two haplotypes common in Britain. This is consistent with long-term British–New Zealand cultural linkages. The origins of the *castaneus* mtDNA sequences widespread in New Zealand are less easy to identify.

Keywords: D-loop; hybridization; mitochondrial DNA; morphology; *Mus musculus*; phylogeography

1. INTRODUCTION

The house mouse (*Mus musculus* L.) originated in the north of the Indian subcontinent *ca* 0.5 Myr ago (Boursot *et al.* 1993), expanded its natural range into the Middle East, and diversified into three major subspecies: *castaneus*; *domesticus*; and *musculus* (Din *et al.* 1996), all intimate commensals. Thereafter, house mice were transported by people wherever they went (Pocock *et al.* 2005). They spread throughout Eurasia, starting in the Neolithic with the development of agriculture and permanent human settlements (Cucchi *et al.* 2005). *Mus musculus domesticus* colonized the Mediterranean basin and western Europe, *musculus* central and eastern Europe and northern Asia, and *castaneus* southern Asia; stable hybrid zones were formed where the subspecies came into contact (Boursot *et al.* 1993).

Since the earliest days of ocean-going navigation, commensal house mice have been carried on ships well beyond this Eurasian range. *Mus musculus domesticus* colonized north and south America, South Africa, Australia and Atlantic archipelagos such as Faroe and Madeira (Berry & Peters 1977; Boursot *et al.* 1993; Gündüz *et al.* 2001). *Mus musculus musculus* and *Mus musculus castaneus* reached several islands in the north Pacific such as Japan and the Hawaiian Islands (Wheeler & Selander 1972; Moriawaki *et al.* 1986).

The global colonization history of the house mouse has been complex, and much about it remains unknown. Here, we provide the first detailed investigation of mice on the archipelago the most distant from Eurasian source areas: New Zealand and its outlying islands in the south west Pacific.

The earliest humans to settle in New Zealand, in *ca* AD 1280 (Wilmshurst *et al.* 2008), were Polynesians migrating from islands which were, at that time, apparently mouse free (Worthy & Holdaway 1996; Steadman 2006). The origins of house mice in New Zealand are therefore generally assumed to be associated with the voyages of early European explorers and traders, facilitated by James Cook's first coastal chart of 1769–1770.

We have applied a genetic approach (Searle 2008) to study the colonization of New Zealand by house mice, using mitochondrial (mt) DNA sequences, nuclear molecular markers and morphology (external measurements, skull features and pelage coloration). The genetic diversity is striking: genetic contributions of all three subspecies of house mouse are present in New Zealand, deriving from different parts of Europe and from Asia. These subspecies have hybridized to create a genetic melting pot that illustrates graphically how easily humans can unwittingly transport and bring together highly divergent genetic forms of single species.

2. MATERIAL AND METHODS

(a) Sample collection

We examined a total of 755 mice, representing 22 field localities in New Zealand (figure 1). Sub-samples were used

* Author for correspondence (jbs3@york.ac.uk).

† These authors contributed equally to the study.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0959> or via <http://journals.royalsociety.org>.

Figure 1. Map showing house mouse collection localities in New Zealand and its outlying islands. The populations or groups of populations sampled for molecular analysis are labelled 1–17 (open circles on New Zealand; precise locations unknown on the outlying islands). Pies show the frequencies of mtDNA haplotypes; these have been grouped by lineage (figure 2). The localities used for morphological analysis are labelled A–H; in some cases the use was made of the same populations as for molecular analysis, in other cases not (closed circles). For sample sizes and further details see appendix 1 in the electronic supplementary material. Note that Campbell is the only large outlying island that currently lacks house mice.

for analyses of coat colour, external measurements, skull characters and molecular traits, as listed in appendices 1–3 in the electronic supplementary material.

(b) Molecular methods and analysis

Specimens for molecular analysis were stored frozen (-80°C) or in absolute ethanol. Genomic DNA was extracted by phenol:chloroform or with commercial extraction kits. Subspecies were distinguished from

mtDNA and nuclear sequences, and mtDNA sequences were used to infer more specific source areas of the colonists.

The complete mt D-loop and flanking regions were amplified with the PCR primers and conditions as described in Gündüz *et al.* (2000) or with the primer pairs L15320/H15782 and L15735/H00072 of Prager *et al.* (1993). The fragments generated were sequenced in both directions using the same primers.

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 15363 and 16295 (933 bp) of Bibb *et al.* (1981). These were then truncated to a standard length of 853 bp, between positions 15424 and 16276, so that we could analyse our data together with the relevant sequences already in GenBank. Our sequences have also been deposited there (FM211632–FM211645). Both the new and previous sequences were readily classified according to subspecies *M. m. domesticus*, *M. m. musculus* and *M. m. castaneus* (e.g. Prager *et al.* 1996; Ihle *et al.* 2006).

The phylogenetic analysis of *M. m. domesticus* is the same as that reported in the companion paper (Searle *et al.* 2009) that provides the detailed results. The analysis involved all *domesticus* sequences from New Zealand together with all published sequences of the same subspecies. GenBank sequences *M. m. gentilulus* AF074545, AF074544; *M. m. castaneus* EF108342, AF088879, AJ286322 and *M. m. musculus* U47504, U47532 were used as outgroups, following Rajabi-Maham *et al.* (2008; *M. m. gentilulus* is a tentative Arabian subspecies described by Prager *et al.* 1998). We also followed Rajabi-Maham *et al.* (2008) in carrying out a Bayesian analysis, generating a 50 per cent majority-rule consensus phylogenetic tree with MRBAYES (Huelsenbeck & Ronquist 2001) based on a GTR+I+ Γ substitution model (selected by MODELTEST v. 3.7: Posada & Crandall 1998) and with the following conditions: 30 per cent burn-in, 5 million generations, two runs of five chains and temperature of 0.2.

The phylogenetic analysis of *M. m. musculus* and *M. m. castaneus* comprised the relevant New Zealand sequences together with all other *musculus* and *castaneus* sequences available in the literature (with *domesticus* AJ286321 as outgroup). The Bayesian analysis involved the same substitution model and run conditions as for the *domesticus* tree. Previous D-loop phylogenies with these subspecies have used the neighbour-joining (NJ) and maximum-parsimony (MP) methods (Prager *et al.* 1996; Gündüz *et al.* 2000) and we adopted those approaches here as well. The NJ tree was also based on the substitution model selected by MODELTEST with bootstrap values from 10 000 replicates. The MP analysis was conducted by heuristic search using the TBR swapping algorithm with 10 random repetitions. A 50 per cent majority-rule consensus tree was constructed with bootstrap values from 1000 replicates using 10 random repetitions for each replicate.

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.

Four nuclear molecular markers with fixed differences between *M. m. domesticus* and *M. m. musculus* were typed for 56 mice (*Abpa*, *Btk*, *D11 cenB2* and *Zfy2*). *Mus musculus castaneus* acts either as *domesticus* (*D11 cenB2*) or as *musculus* (*Abpa*, *Btk*, *Zfy2*). Controls of known *domesticus* (from England), *musculus* (Czech Republic) and *castaneus* (Thailand) were used to check all markers identified in New Zealand material. The *Abpa* marker is a sequence within the androgen-binding protein alpha subunit, 10 cM from the centromere of chromosome 7, scored as in Dod *et al.* (2005). The *Btk* marker is defined as the presence or absence of the B1 insertion between positions 77329–77464 in the Bruton's agammaglobulinemia tyrosine kinase gene

on the X chromosome, scored as in Munclinger *et al.* (2002). *D11 cenB2* is a marker at the centromeric region of chromosome 11, typed according to the method of Lanneluc *et al.* (2004), but the reaction to detect *musculus* requires a higher annealing temperature of 64°C. The *Zfy2* marker is defined as the presence or absence of an 18 bp deletion in the last exon of the Zinc finger protein 2 on the Y chromosome, scored on males ($n=25$) according to the protocol of Orth *et al.* (1996).

(c) Morphological analysis

Freshly collected mice of all ages were scored for dorsal and ventral coat colour using Munsell standard soil colour charts. Only fully grown adults of Lidicker's tooth wear classes 4 and above (illustrated in Ruscoe & Murphy 2005) were used to score other characteristics. Tail length was determined by the hanging tail method (Jewell & Fullagar 1966) and head and body length by subtraction from total length. Relative tail length was expressed as tail : body length ratio (TBLR). Skulls were scored for general skull shape, shape of the zygomatic plate, shape of the suture between the squamosal and parietal bones, and shape of the first lower molar, four features that distinguish *M. m. domesticus* from *M. m. musculus* in Europe (Marshall & Sage 1981; Kraft 1985). Skull morphology of *M. m. castaneus* is less well known, so was not separately classified.

3. RESULTS

(a) MtDNA analysis

MtDNA haplotypes of all three subspecies of house mouse were found on the New Zealand mainland and its outlying islands (appendices 1 and 2 in the electronic supplementary material). At 11 of 17 localities sampled for our molecular analysis (figure 1), we obtained only *domesticus* sequences; at one, both *musculus* and *castaneus* sequences, and at five, only *castaneus* sequences. Altogether, 10 *domesticus* haplotypes were found in 82 mice, one *musculus* haplotype in two mice, and three *castaneus* haplotypes in 22 mice.

The New Zealand *domesticus* haplotypes were distributed in five places in the phylogenetic tree (figure 2a). Haplotypes domNZ.1–5 fit within a well-supported lineage (posterior probability of 0.96) best documented in Britain and Germany (Searle *et al.* 2009). Of the 55 mainland New Zealand house mice with *domesticus* mtDNA included in this study, 47 belonged to this lineage, as did the 16 specimens from Auckland Island and Macquarie Island (figure 1). Haplotype domNZ.4 that is identical to one of the common haplotypes found in Britain and Germany (BritIsl.5; Searle *et al.* 2009), was particularly numerous (45 mice) and widely distributed in New Zealand. Likewise, domNZ.1 is identical to a common Anglo-German haplotype (BritIsl.1; Searle *et al.* 2009) and is frequent (15 mice) and widespread in New Zealand (North and South Islands and outlying islands). Haplotype domNZ.3 (found in one location in New Zealand) is identical to U47432 (found in one location in Germany) and both become identical to a British haplotype (U47434 found in one location) when truncated for phylogenetic analysis.

Haplotypes domNZ.6–10 are distributed elsewhere in the tree (figure 2a). The haplotypes domNZ.9 and 10 found at Ruatangata and Ashburton are part of the

Figure 2. Phylogenetic trees for (a) *M. m. domesticus* and (b) *M. m. castaneus* and *M. m. musculus*, after Bayesian analysis (see text). Trees show all house mouse haplotypes found in New Zealand together with all available haplotypes from GenBank. All posterior probabilities of 0.60 or greater are shown for branches leading to New Zealand haplotypes.

‘Orkney’ lineage that consists predominantly of house mice from Ireland and the extreme north of Britain, although domNZ.9 is actually identical to a sequence

previously found in a mouse from Croatia (see Searle *et al.* 2009). One haplotype on North Island (domNZ.6, represented by two individuals from Taranaki) has an

affiliation with continental Europe (northern Italy, Germany); domNZ.8 from Antipodes Island has the closest affinity with a haplotype from Spain; and domNZ.7 from Pitt Island is basal within the tree.

Considering all New Zealand specimens with *domesticus* mtDNA, the haplotype diversity ($h \pm \text{s.d.}$) is 0.66 ± 0.05 and the nucleotide diversity ($\pi \pm \text{s.d.}$) is 0.0042 ± 0.0010 .

Figure 2b shows the phylogenetic tree for *musculus* and *castaneus* (a more detailed version is available in appendix 4 in the electronic supplementary material). The single *musculus* haplotype found in Wellington (figure 1) was identical to sequences previously described from central Europe (southern Germany, Austria and Croatia) and in the same weakly supported lineage (posterior probability of 0.74) as others from the same geographical region. This lineage was also identified with NJ and MP analyses with less than 50 per cent bootstrap support.

Mus musculus castaneus mtDNA haplotypes were found in southern parts of both North and South Islands (casNZ.1 and 3) and on Chatham Island (casNZ.2). The three New Zealand *castaneus* haplotypes all belong to the same well-supported lineage (posterior probability of 0.98), also present with high bootstrap support, 91 per cent and 92 per cent, in the NJ and MP trees, respectively. The two other sequences in this lineage were derived from Pakistan and Thailand.

(b) Analysis of nuclear molecular markers

Fifty-five out of 77 mice from all 12 mainland New Zealand localities used for mtDNA analysis (figure 1) were also typed for nuclear molecular markers (appendix 1 in the electronic supplementary material). The vast majority of mice could be scored as *domesticus* with these markers. This group includes the male mouse from Wellington with *musculus* mtDNA for which all four nuclear markers could be scored as *domesticus*, and 17 individuals with *castaneus* mtDNA (five from Wellington and three each from Dunedin, Borland, Grebe and southern Fiordland) for which three or four nuclear markers could be scored as *domesticus*, depending on whether the individuals were females (seven mice, three markers) or males (10 mice, usually four and sometimes three markers).

Only mice from Nelson Lakes National Park in northern South Island showed any definite nuclear genetic input from *musculus* and/or *castaneus*. Four came from Lake Rotoiti and two from Mount Misery, 20 km away (the two Nelson Lakes populations in figure 1). One male from Rotoiti had a *castaneus*- or *musculus*-specific *Zfy2* product for the Y chromosome, but could be scored as *domesticus* for the X-chromosome marker and two autosomal markers. Four of the five females also had hybrid genomes. One from Rotoiti was heterozygous at the *D11 cenB2* locus, having a *musculus* type allele and a *domesticus/castaneus* allele; two (one from each locality) were heterozygotes for a *castaneus* or *musculus* allele and a *domesticus* allele at the *Btk* locus on the X chromosome; and one from Mount Misery was homozygous for a *castaneus* or *musculus* allele at the *Btk* locus. At other markers these four females could be scored as *domesticus*, and one female from Rotoiti could be scored as *domesticus* at all loci.

(c) Morphological analysis

Pelage coloration was scored in a total of 277 fresh house mice from mainland New Zealand (appendix 3 in the

electronic supplementary material). Dorsally, almost all were brown (32%) or dark brown (64%) with a few grey. Ventral colour ranged from white through grey to brown, most commonly pale brown (59%). The most frequent combination was a dark brown back and a pale brown belly (56%). Both this form and the variation around it are observed among *domesticus* from western Europe (Sage 1981). *Mus musculus musculus* more typically has a whitish belly (Boursot et al. 1993). *Mus musculus castaneus* tends to have an ochraceous tint (Marshall & Sage 1981), but that was not observed in any New Zealand mice. However, coloration is variable in all three subspecies and this character is not diagnostic.

More reliable as a discriminator between subspecies is relative tail length (*musculus* tends to have a smaller TBLR than the other two subspecies; Marshall & Sage 1981; Boursot et al. 1993). The New Zealand TBLR mean was 0.991 (range 0.67–1.30), compared with 0.872 (0.74–0.91) for *musculus* and 1.014 (0.87–1.20) for *domesticus* from continental Europe (Kraft 1985). The difference between the mean New Zealand and European values was significant for *musculus* ($t_{163} = -5.033$, $p < 0.001$) but not for *domesticus* ($t_{166} = 1.888$, $p = 0.061$). There was significant local variation in TBLR values between the eight largest samples from New Zealand (figure 3; $p < 0.001$, one-way ANOVA); all of them were significantly different in TBLR from European *musculus*, but none from *domesticus*.

Each of the four features discriminating *domesticus* from *musculus* was scored in 549 skulls of New Zealand mice, as listed in appendix 1 in the electronic supplementary material. The distribution of these scores for the eight largest samples, plotted against TBLR in figure 3, was strongly skewed towards the reference values for *domesticus* (TBLR = 1.014, skull score 0) as opposed to those for *musculus* (TBLR = 0.872, skull score 4); the mean skull score was 0.661. However, the plots reveal deviation away from the *domesticus* morphology in samples from throughout the country, including places such as Pureora and Mana Island for which no genetic data are yet available.

4. DISCUSSION

(a) Taxonomy of New Zealand house mice and evidence of hybridization

Our morphological and molecular data suggest that the house mice of New Zealand should be classified as the western European subspecies *M. m. domesticus* (see also Ruscoe & Murphy 2005). Most of the individuals examined were typed as *domesticus* on all criteria scored. However, there was also definitive evidence of the genetic presence of the other two subspecies as follows:

- (i) we found mt D-loop sequences characteristic of south Asian *M. m. castaneus* on both North and South Islands and on one outlying island (Chatham) and
- (ii) we found mt D-loop sequences identical to central European *M. m. musculus* in one locality on North Island (Wellington).

Furthermore, based on the evidence from three out of four nuclear markers, non-*domesticus* genes were also present in most individuals at two separate locations in

Figure 3. Morphological characters of New Zealand house mice as illustrated with data from eight large samples (see figure 1 and appendix 1 in the electronic supplementary data). TBLR, tail : body length ratio. Skull scores 0–4 defined from four characters distinguishing *M. m. domesticus* from *M. m. musculus* in Europe. Panel of reference data: left: *M. m. domesticus*, TBLR=1.014, skull score 0 (Kraft 1985); centre: overall data for New Zealand; right: *M. m. musculus*, TBLR=0.872, skull score 4 (Kraft 1985). Other panels: circles, females; triangles, males.

Nelson Lakes National Park on South Island and one of these mice carried a definitive *musculus* allele. Data on relative tail length were also consistent with a low level but probably widespread presence of elements of the *musculus* nuclear genome on both North and South Islands (figure 3). Generally the skulls of New Zealand mice were similar to European *domesticus*, but features characteristic of *musculus* were found at low frequency in many localities.

Considering the house mice collected on mainland New Zealand, it is important to emphasize that whenever there was either a *musculus* or *castaneus* element to the genome, there was also a *domesticus* element. Mainland New Zealand was dominated by *domesticus*; genomic contributions of the other subspecies were present only in hybrids.

Our results demonstrate that New Zealand is a genetic melting pot for house mice at the subspecies level. But the same is also true for the divergent lineages within the *domesticus* subspecies. Across the archipelago, we found four different *domesticus* mtDNA lineages plus a single basal haplotype (figure 2a), and at three localities (Ruatangata, Taranaki and Ashburton) two different *domesticus* lineages were present (figure 1). Hence, the nucleotide diversity (π) for *domesticus* mtDNA for our New Zealand material was relatively high at 0.0042. By contrast, the haplotype diversity (h) was relatively low at 0.66, largely because haplotype domNZ.4 was so abundant. The equivalent values for the Madeiran archipelago were $\pi=0.0014$ and $h=0.90$ (Gündüz *et al.* 2001). Continental *domesticus* populations tend to have higher values for both haplotype and nucleotide diversity. For example, Gündüz *et al.* (2005) estimated $\pi=0.0084$ and $h=0.98$ from 98 mice representing 48 localities in Turkey (see also Rajabi-Maham *et al.* 2008).

The interplay of divergent genomes within populations and individuals is of great theoretical interest

(Arnold 2006). The house mouse in New Zealand offers particular opportunities for analysis, given the presence of genes of three different subspecies, multiple genealogical lineages within one of those subspecies, and the huge data resources available for genome studies of house mice (Mouse Genome Sequencing Consortium 2002). So, the house mouse in New Zealand is a potentially valuable model for future work on the fundamentals of genome interaction to contrast, for example, with mice from Japan, which show mixed *musculus/castaneus* genomes (Terashima *et al.* 2006).

(b) Colonization history of New Zealand house mice

Any account of the colonization history of house mice in New Zealand needs to explain (i) the dominance of *M. m. domesticus* belonging to mtDNA haplotypes with affinities to house mice from the British Isles (domNZ.1–5, 9–10), (ii) the presence of *M. m. musculus* based on morphology, nuclear markers and mtDNA (musNZ.1), the latter indicating central European affiliations, and (iii) the presence of *M. m. castaneus* mtDNA (casNZ.1–3) with a southern Asian affinity. Ships infested with mice have arrived throughout the 240-year European maritime history of New Zealand, so the following scenario needs to be viewed in that context.

In 1769, James Cook was the first of several European explorers to land in New Zealand; his expedition was followed by others from Britain, France and Spain (King 2003). The exploitation of the resources of New Zealand by European traders based at Sydney (then called Port Jackson, established 1788) began very early. The British East India Company was making use of New Zealand timber and flax by 1790 (King 2003), and sealers and whalers of different nationalities started working in New Zealand waters well before 1800 (Ross 1987;

Smith 2002). Long before the beginning of organized colonization in 1840, New Zealand was already part of an extensive trading network also including ports in Europe, southern Asia and Australia (Ross 1987).

From the earliest days of European contact (Thomson 1922; King 2003), house mice began to exploit human settlements in New Zealand, as they do throughout the world (Boursot *et al.* 1993). In addition, the absence of close competitors (Cucchi *et al.* 2005) allowed house mice to live as non-commensals, and they are now found in natural habitat throughout New Zealand (Ruscoe & Murphy 2005). Shipwrecks and strandings in unpeopled areas were common (2300 shipwrecks along the New Zealand coast recorded since 1795: Ingram 2007), and provided additional opportunities for mice to reach remote areas. Indeed, the first record of house mice in New Zealand was on Ruapuke Island (figure 1) after the 1824 stranding and subsequent salvage of the *Elizabeth Henrietta*, an Australian brig bringing 'British manufactures' from Sydney to the Maori in exchange for flax (McNab 1908, p. 648). Mice were present at the port of Russell in the Bay of Islands (figure 1) in or before the 1830s (Guthrie-Smith 1969).

Most ships arriving in New Zealand during the early mid-nineteenth century came from Britain, and they usually called at Cape Town, Sydney and other Australian ports on the way (Jamieson 2001). The influx of settlers and their companion animals increased rapidly: 500 000 had arrived by 1881 (King 2003). In the first 50 years, 49 per cent of immigrants were from England and Wales, 24 per cent from Scotland, 19 per cent from Ireland, and the rest from Germany, Scandinavia, Poland, France and Italy (King 2003). The immigrant ships, their cargo, provisions and livestock and the subsequent close mutual trading links between Europe, Australia and New Zealand, provided decades of multiple opportunities for colonization by European mice resident in ports of origin and transit.

Asian mice could have reached New Zealand by one or all of at least three different routes: (i) between 1792 and 1820, indirectly with Sydney-based sealers and traders returning from the Canton fur market (Ross 1987; Smith 2002), (ii) after 1869, directly with Chinese gold miners from Canton (King 2003), or (iii) since the 1960s, on Asian fishing vessels after the restrictions on their use of New Zealand's ports have been lifted (Johnson 2004). Since 1985, ship rats (*Rattus rattus*) of the Asian karyotype have occasionally reached New Zealand with the Asian fleet (Innes 2005), and, presumably, so could Asian mice.

Given this history, we suggest the following scenario explaining the derivation of the contemporary house mice of New Zealand from different subspecies and source areas.

- (i) *Mus musculus domesticus* from the British Isles. New Zealand was explored, exploited and settled very largely by people from the British Isles, directly or via Australia, so the predominant presence of house mice with a *domesticus* morphology and genome, and the widespread presence of seven mtDNA haplotypes (domNZ.1–5, 9 and 10) belonging to lineages found in the British Isles, are both consistent with documentary history. The fact that two of the most common and widespread

haplotypes in New Zealand (domNZ.1 and 4) are the same as two of the most common and widespread haplotypes in Britain (BritIsl.1 and 5, respectively) makes the case even stronger. Not only do these haplotypes occur on North and South Islands, they are also found on Auckland and Macquarie Islands. Between 1770 and 1840, domNZ.1 and 4 and other haplotypes with close links to the British Isles had multiple opportunities to spread from Sydney, both to pre-colonial New Zealand and to Auckland Island, discovered in 1806, and Macquarie Island, discovered in 1810 (Clark & Dingwall 1985). Among the other haplotypes to arrive in New Zealand was domNZ.9. Although this haplotype is within the Orkney lineage, it has actually been recorded in Croatia rather than the British Isles and further studies are needed to establish the basis of this intriguing result.

- (ii) *Mus musculus musculus* from central Europe. The single *musculus* D-loop sequence from Wellington, identical to one recorded from Germany, Austria and Croatia, suggests a central European source. Wellington was one of the earliest settler ports (4000 immigrants by 1843: King 2003), and now, as New Zealand's capital city, hosts many resident members of the international diplomatic corps, providing ample opportunity for arrival of house mice of central European derivation. The occurrence of a *musculus* nuclear marker within Nelson Lakes National Park is also consistent with known history: the largest of the minority settler groups, the Germans, gathered in the Nelson district (King 2003).
- (iii) *Mus musculus castaneus*. The source area for the S Asian *castaneus* mtDNA haplotypes found in the southern parts of both South and North Islands (casNZ.1, 3) is ill defined, and offers no clues to their origin. Clearly, a more detailed phylogeny for *castaneus* would be desirable to make progress on this point. The mice of Chatham Island also have *castaneus* D-loop sequences, though a different haplotype (casNZ.2) from those recorded on the mainland. The ancestors of the Chatham Island mice could have got ashore in cargo from the 1853 wreck of the *Randolph*, an English barque trading from China to the Chathams via Melbourne (Ingram 2007). Additional colonizations might have come, either previously from the mainland (800 km west), or more recently via the numerous Asian fishing boats that now visit Waitangi, the main port on Chatham Island. It is notable that mice from nearby Pitt Island are characterized by a *domesticus* mtDNA haplotype (figure 1). This most likely reflects a differing colonization history but in this and other cases the possible involvement of lineage sorting (Avice 2000) cannot be discounted.

The scenario that we have developed is tentative, and cannot at this stage allow for the many unknown factors that complicate interpretation of the colonization history of New Zealand house mice, such as the influence of transit ports (e.g. in Australia) and transport within New Zealand itself. More information is needed both to

test the interpretations that we suggest for the mainland and to attempt adequately to explain the distribution of mtDNA haplotypes on the outlying islands. However, mice are exceptionally pervasive commensals, so it is certain that the New Zealand archipelago has been 'moused' from all over the world, in the same way as it has been 'peopled'.

We are extremely grateful to Kath Walker, Graeme Taylor and Alex McKillop for collecting mice from the offshore islands, to Tasmania Parks and Wildlife Service (Keith Springer) for the Macquarie Island specimens and to Pavel Munclinger for his advice and preliminary typing with nuclear markers. We also thank Alec Zwart for statistical help, Rhys Richards for advice on maritime history, Jaroslav Piálek and François Catzeffis for provision of samples of known subspecies, Friða Jóhannesdóttir for drawing the trees and commenting on the manuscript, and Max Oulton for drawing the map. Funding was provided by the Universities of Waikato and York, and the Scientific and Technological Research Council of Turkey (TÜBİTAK). Part of this work was carried out using the resources of the Computational Biology Service Unit from Cornell University which is partially funded by Microsoft Corporation.

REFERENCES

- Arnold, M. L. 2006 *Evolution through genetic exchange*. Oxford, UK: Oxford University Press.
- Avice, 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)
- 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)
- Boursot, P., Auffray, J.-C., Britton-Davidian, J. & Bonhomme, F. 1993 The evolution of house mice. *Annu. Rev. Ecol. Syst.* **24**, 119–152. (doi:10.1146/annurev.es.24.110193.001003)
- Clark, M. R. & Dingwall, P. R. 1985 *Conservation of islands in the Southern Ocean: a review of the protected areas of Insulantarctica*. Wellington, New Zealand: Department of Lands and Survey, for IUCN.
- Cucchi, T., Vigne, J.-D. & Auffray, J.-C. 2005 First occurrence of the house mouse (*Mus musculus domesticus* Schwarz & 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)
- Din, W. *et al.* 1996 Origin and radiation of the house mouse: clues from nuclear genes. *J. Evol. Biol.* **9**, 519–539. (doi:10.1046/j.1420-9101.1996.9050519.x)
- Dod, B., Smadja, C., Karn, R. C. & Boursot, P. 2005 Testing for selection on the androgen-binding protein in the Danish mouse hybrid zone. *Biol. J. Linn. Soc.* **84**, 447–459. (doi:10.1111/j.1095-8312.2005.00446.x)
- 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.
- 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)
- Guthrie-Smith, H. 1969 *Tutira: the story of a New Zealand sheep station*. Wellington, New Zealand: A. H. and A. W. Reed.
- 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)
- Ingram, C. W. N. 2007 *New Zealand shipwrecks: over 200 years of disasters at sea*. Auckland, New Zealand: Hodder Moa.
- Innes, J. G. 2005 Ship rat. In *The handbook of New Zealand mammals* (ed. C. M. King), pp. 187–203. Melbourne, Australia: Oxford University Press.
- Jamieson, P. 2001 The taxonomic identification of the New Zealand house mouse. MSc thesis, University of Waikato, Hamilton, New Zealand.
- Jewell, P. A. & Fullagar, P. J. 1966 Body measurements of small mammals: sources of error and anatomical changes. *J. Zool.* **150**, 501–509.
- Johnson, D. 2004 *Hooked: the story of the New Zealand fishing industry*. Christchurch, New Zealand: Hazard Press.
- King, M. 2003 *The Penguin history of New Zealand*. Auckland, New Zealand: Penguin Books.
- Kraft, R. 1985 Morphological characteristics and distribution of the house mouse *Mus musculus musculus* L., 1758, and *Mus musculus domesticus* Ratty, 1772 (Rodentia, Muridae) in Bavaria. *Säugetierk. Mitt.* **32**, 1–12.
- Lanneluc, I., Desmarais, E., Boursot, P., Dod, B. & Bonhomme, F. 2004 Characterization of a centromeric marker on mouse chromosome 11 and its introgression in a *domesticus/musculus* hybrid zone. *Mamm. Genome* **15**, 924–934. (doi:10.1007/s00335-004-2397-x)
- Marshall, J. T. & Sage, R. D. 1981 Taxonomy of the house mouse. *Symp. Zool. Soc. Lond.* **47**, 15–25.
- McNab, R. (ed.) 1908 *Historical records of New Zealand*, vol. 1. Wellington, New Zealand: Government Printer.
- Moriwaki, K., Miyashita, N., Suzuki, H., Kurihara, Y. & Yonekawa, H. 1986 Genetic features of major geographical isolates of *Mus musculus*. *Curr. Top. Microbiol. Immunol.* **127**, 55–61.
- Mouse Genome Sequencing Consortium 2002 Initial sequencing and comparative analysis of the mouse genome. *Nature* **420**, 520–562. (doi:10.1038/nature01262)
- Munclinger, P., Božíková, E., Šugerková, M., Piálek, J. & Macholán, M. 2002 Genetic variation in house mice (*Mus*, Muridae, Rodentia) from the Czech and Slovak Republics. *Folia Zool.* **51**, 81–92.
- Nei, M. 1987 *Molecular evolutionary genetics*. New York, NY: Columbia University Press.
- Orth, A., Lyapunova, E., Kandaurov, A., Boissinot, S., Boursot, P., Vorontsov, N. & Bonhomme, F. 1996 L'espèce polytypique *Mus musculus* en Transcaucasie. *C. R. Acad. Sci. III Sci. Vie* **319**, 435–441.
- Pocock, M. J. O., Haufler, 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., Gyllenstein, 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)
- Ross, J. O. C. 1987 *William Stewart: sealing captain, trader and speculator*. Canberra, Australia: Roebuck Society.
- Ruscoe, W. A. & Murphy, E. C. 2005 House mouse. *The handbook of New Zealand mammals* (ed. C. M. King), pp. 204–221, 2nd edn. Melbourne, Australia: Oxford University Press.
- Sage, R. D. 1981 Wild mice. In *The mouse in biomedical research*, vol. 1 (eds H. L. Foster, J. D. Small & J. G. Fox), pp. 39–90. New York, NY: Academic Press.
- Searle, J. B. 2008 The genetics of mammalian invasions: a review. *Wildlife Res.* **35**, 185–192. (doi:10.1071/WR07123)
- Searle, J. B. *et al.* 2009 Of mice and (Viking?) men: phylogeography of British and Irish house mice. *Proc. R. Soc. B* **276**, 201–207. (doi:10.1098/rspb.2008.0958)
- Smith, I. W. G. 2002 *The New Zealand sealing industry: history, archaeology, and heritage management*. Wellington, New Zealand: Department of Conservation.
- Steadman, D. W. 2006 *Extinction and biogeography of tropical Pacific birds*. Chicago, IL: University of Chicago Press.
- 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)
- Terashima, M., Furusawa, S., Hanzawa, N., Tsuchiya, K., Suyanto, A., Moriwaki, K., Yonekawa, H. & Suzuki, H. 2006 Phylogeographic origin of Hokkaido house mice (*Mus musculus*) as indicated by genetic markers with maternal, paternal and biparental inheritance. *Heredity* **96**, 128–138. (doi:10.1038/sj.hdy.6800761)
- Thomson, G. M. 1922 *The naturalisation of animals and plants in New Zealand*. Cambridge, UK: Cambridge University Press.
- Wheeler, L. L. & Selander, R. K. 1972 Genetic variation in populations of the house mouse, *Mus musculus* in the Hawaiian islands. *Stud. genet. VII Univ. Texas Publ.* **7213**, 269–296.
- Wilmshurst, J. M., Anderson, A. J., Highham, T. F. G. & Worthy, T. H. 2008 Dating the prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proc. Natl Acad. Sci. USA* **105**, 7676–7680. (doi:10.1073/pnas.0801507105)
- Worthy, T. H. & Holdaway, R. N. 1996 Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. *J. R. Soc. NZ* **26**, 275–361.