



Glacial survival or late glacial colonization? Phylogeography of the root vole (*Microtus oeconomus*) in north-west Norway

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ABSTRACT

Aim It has been proposed that the root vole subspecies, *Microtus oeconomus finmarchicus*, survived the last glacial period on islands on the north-west coast of Norway. The Norwegian island of Andøya may have constituted the only site with permanent ice-free conditions. Geological surveys and fossil finds from Andøya demonstrate that survival throughout the last glacial maximum was probably possible for some plants and animals. In this study we aim to infer the recent evolutionary history of Norwegian root vole populations and to evaluate the glacial survival hypothesis.

Methods DNA sequence variation in the mitochondrial cytochrome *b* gene was studied in 46 root voles from 19 localities.

Location Northern Fennoscandia and north-west Russia with a focus on islands on the north-west coast of Norway.

Results The phylogeographical analyses revealed two North European phylogroups labelled 'Andøya' and 'Fennoscandia'. The Andøya phylogroup contained root voles from the Norwegian islands of Andøya, Ringvassøya and Reinøya and two localities in north-west Russia. The Fennoscandian phylogroup encompassed root voles from the three Norwegian islands of Kvaløya, Håkøya and Arnøya and the remaining specimens from Norway, northern Sweden and Finland. Nucleotide diversity within the Andøya and Fennoscandian phylogroups was similar, ranging from 0.5% to 0.7%.

Main conclusions Both our genetic data and previously published morphological data are consistent with *in situ* glacial survival of root voles on Andøya during the last glacial maximum. However, the level of genetic diversity observed in the extant island populations, the past periods of severe climatic conditions on Andøya and the ecology of the root vole are somewhat difficult to reconcile with this model. A biogeographical scenario involving late glacial recolonization along the northern coasts of Russia and Norway therefore represents a viable alternative. Our results demonstrate that complex recolonization and extinction histories can generate intricate phylogeographical patterns and relatively high levels of genetic variation in northern populations.

Keywords

Andøya, colonization history, cytochrome *b*, glacial refugia, *Microtus oeconomus*, mtDNA, north-west Norway, nunatak model.

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INTRODUCTION

There is an ongoing debate concerning the number and location of the latest (Weichselian) glacial refugia in Eurasia. In

particular, it has been suggested that some European populations originate from refugia in central and eastern Europe and/or Asia (Bilton *et al.*, 1998; Horáček, 2000; Stewart & Lister, 2001) and not only the Mediterranean peninsulas and

Caucasus as suggested traditionally (Hewitt, 1996, 2000; Taberlet *et al.*, 1998). The model of more northern glacial survival is supported by genetic and fossil evidence in several vole species (Jaarola & Searle, 2002; Brunhoff *et al.*, 2003; Deffontaine *et al.*, 2005) as well as genetic surveys in a wide range of organisms such as plants (e.g. Palmé *et al.*, 2003; Schönswetter *et al.*, 2005), fishes (e.g. Kotlik & Berrebi, 2001; Hänfling *et al.*, 2002), amphibians (Wallis & Arntzen, 1989; Rafinski & Babik, 2000) and invertebrates (Haase *et al.*, 2003).

In North America, glacial refugia also existed north of the Weichselian (Wisconsin) ice sheet. Eastern Beringia undoubtedly represented an important refugium in the north-west (e.g. Fedorov *et al.*, 1999a,b; Barnes *et al.*, 2002; Brunhoff *et al.*, 2003; Galbreath & Cook, 2004) and some Arctic plants and mammals may also have survived in local ice-free areas in the eastern Canadian Arctic and/or northern Greenland (e.g. Abbott *et al.*, 2000; Fedorov & Stenseth, 2002; Waltari & Cook, 2005). In Europe, high-latitude refugia within or next to the Late Weichselian ice sheet in Scandinavia have been suggested. This model of *in situ* glacial survival, or the nunatak hypothesis, was originally postulated in the 19th century in order to explain the fragmented distribution of some species in the Scandinavian mountain flora (see references in Alm & Birks, 1991; Brochmann *et al.*, 2003). The glacial survival hypothesis has remained extremely controversial. Today, many researchers consider it superfluous since plant microfossil and genetic data imply that current distribution patterns can be adequately explained by the *tabula rasa* hypothesis, stating that all present-day populations trace their origin to post-glacial immigration and hybridization (Birks, 1994; Gabrielsen *et al.*, 1997; Tollefsrud *et al.*, 1998; Brochmann *et al.*, 2003). However, recent studies on tree macrofossils (Kullman, 2000, 2002, 2006) as well as genetic analyses of the Norwegian lemming (*Lemmus lemmus*; Fedorov & Stenseth, 2001) suggest that the *in situ* model cannot be totally dismissed. Glacial survival in west Norway has also been suggested recently for, for example, a woodland grass (*Melica nutans*; Tyler, 2002) and a lichen (Printzen *et al.*, 2003) but these conclusions are much more speculative (cf. Brochmann *et al.*, 2003).

The last glacial maximum (LGM) 21,000–17,000 yr BP (Andersen & Borns, 1997) represents the critical period for the *in situ* survival hypothesis. Large ice-free areas existed in Fennoscandia during periods of the last glaciation (Ukkonen *et al.*, 1999; Svendsen *et al.*, 2004), but Fennoscandia was almost completely covered by the Eurasian ice sheets at the LGM (cf. Svendsen *et al.*, 2004). In fact, because of its close position to the shelf break, the northern part of the island of Andøya in the Lofoten-Vesterålen archipelago in north-west Norway (Fig. 1) may have constituted the only site along the Norwegian coastline with permanent ice-free conditions during the last glaciation (Vorren, 1978; Vorren *et al.*, 1988; Møller *et al.*, 1992; C. Hjort, personal communication). Recent geological and palaeontological studies of Andøya indicate that *in situ* glacial survival throughout the LGM may have been possible for some hardy species. Although the fossil records cannot provide definite evidence of continuous vegetation on

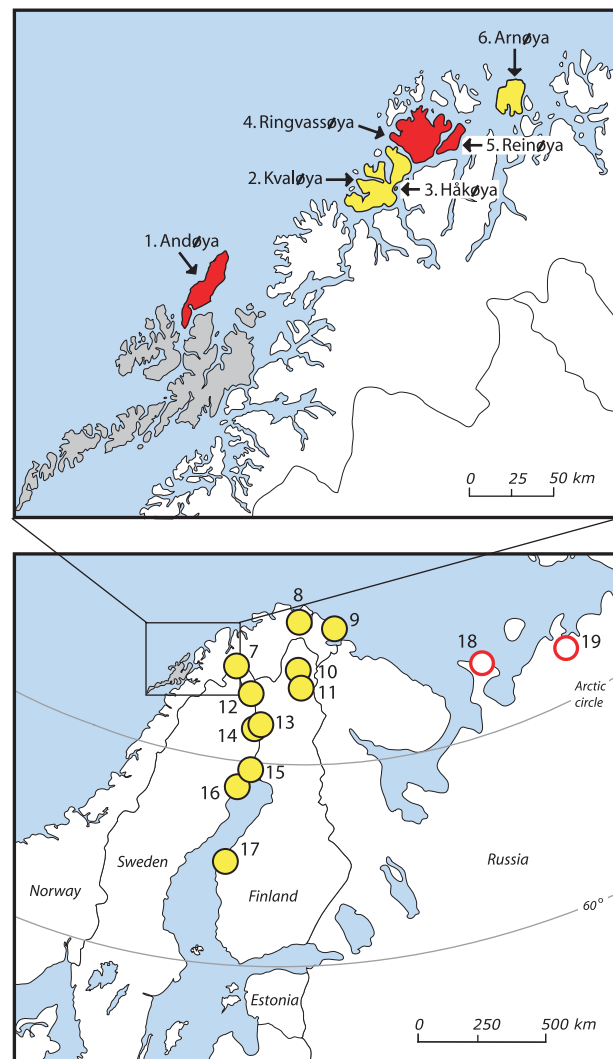


Figure 1 Sampling localities of root voles (*Microtus oeconomus*). Numbers correspond to localities (Table 1) and colours to mtDNA phylogroups (see Fig. 2). The Lofoten-Vesterålen archipelago, to which the island of Andøya belongs, is shown in grey.

Andøya, macrofossil findings of plants dated to 22,000–12,800 yr BP demonstrate that there was vegetation on Andøya during the LGM (Alm, 1993; Birks, 1994). Some taxa like grasses (Poaceae), poppy (*Papaver*) and buttercups (*Ranunculus*) are so commonly recorded as fossils that an uninterrupted Late Weichselian presence seems plausible (Alm & Birks, 1991). Records of invertebrate remains from 22,000–19,000 yr BP also point to glacial survival on Andøya (Solem & Alm, 1994). Furthermore, a fossil finding of a stoat (*Mustela erminea*) on Andøya, dated to 15,000 yr BP (Fjellberg, 1978), suggests the presence of small mammals in late glacial times, the carnivorous stoat's most favoured food items being lemmings and voles.

The idea of north Scandinavian refugia was applied to mammals by Ekman (1922), who suggested that the Norwegian lemming (*L. lemmus*) was a relic from the previous, Eemian, interglacial, and that it survived the entire last glaciation (115,000–10,000 yr BP) on the north-west coast of

Norway. This idea was further developed by Siivonen (1968), who argued that subspecies of some small mammals, such as the common shrew (*Sorex araneus bergensis*), the red-backed vole (*Clethrionomys rutilus finmarchicus*) and the root vole (*Microtus oeconomus finmarchicus*) described from islands on the Norwegian coast, also survived the last glaciation *in situ*. The first genetic investigation to point to a local Scandinavian refugium for a small mammal was presented by Fedorov & Stenseth (2001), who suggested that the star-like phylogeny and low mitochondrial (mt) DNA variation in the Norwegian lemming was due to a local bottleneck in Scandinavia during the LGM. In addition, a karyotype study of common shrews in northern Fennoscandia indicates that glacial survival on Andøya may represent a possible scenario for the Ammarnäs chromosome race (Fredga, in press).

Our previous distribution-wide phylogeographical study of sequence variation in the mitochondrial cytochrome *b* gene in root voles (*Microtus oeconomus*) showed that the species is divided into four ancient and largely allopatric mtDNA phylogroups (Brunhoff *et al.*, 2003). In the North European mtDNA phylogroup, root voles from the Norwegian islands Andøya and Ringvassøya demonstrated a closer relationship to specimens from northern Russia than to other Fennoscandian populations. In this study, we performed a detailed investigation of root voles from northern Europe, including Andøya and five other islands in north-west Norway, to elucidate the recent evolutionary history of these root vole populations and to evaluate the glacial survival and *tabula rasa* hypotheses.

MATERIALS AND METHODS

Samples, DNA extraction, polymerase chain reaction and sequencing

Total genomic DNA was extracted from ethanol-preserved root vole tissue samples using the DNeasyTM Tissue Kit (Qiagen, Solna, Sweden). The mtDNA analysis comprised a total of 46 root voles from 19 localities (Fig. 1, Table 1), including 27 voles used in a previous survey (Brunhoff *et al.*, 2003). The entire mitochondrial cytochrome *b* gene (1140 bp) was amplified in a single polymerase chain reaction (PCR) as described by Jaarola & Searle (2002). Direct sequencing was performed in both directions using the PCR primers H15408MO, H15576MO (Brunhoff *et al.*, 2003), L15162M2, H15348A-SP (Jaarola & Searle, 2002) and L15408Marv (Haynes *et al.*, 2003).

Phylogenetic analysis

Sequences were aligned using the SeqManII module of the Lasergene99 program. Phylogenetic analyses were conducted using neighbour-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) algorithms. For the NJ and ML analyses, MODELTEST 3.06 (Posada & Crandall, 1998) was used to establish the model of DNA substitution that best fitted the data. The models selected were the Tamura–Nei model (TrN; Tamura & Nei, 1993) including the proportion of invariable sites (I), and the HKY model (Hasegawa *et al.*, 1985) including I and the gamma shape parameter (α). For

Fig ref.	Locality	Haplotype	N	GenBank accession no.
1	Andøya	Nor-1, Nor-2, Nor-10	3	AY219981, AY219982, DQ452134
2	Kaldfjord, Kvaløya	Nor-3	3	AY219983
2	Sandvik, Kvaløya	Nor-4	2	AY219984
2	Kattfjord, Kvaløya	Nor-11	3	DQ452135
2	Henrikvikdalen, Kvaløya	Nor-12	1	DQ452136
3	Håkøya	Nor-18	3	DQ452142
4	Ringvassøya	Nor-5	3	AY219985
5	Reinøya	Nor-15, Nor-16, Nor-17	3	DQ452139, DQ452140, DQ452141
6	Arnøya	Nor-13, Nor-14	3	DQ452137, DQ452138
7	Kilpisjärvi	Fin-1	3	AY219986
8	Porsanger	Nor-6	3	AY219987
9	Hamningberg	Nor-7	1	AY219988
10	Inari	Fin-Swe	1	AY219989
11	Laanila	Fin-2, Fin-3	3	AY219990, AY219991
12	Muonio	Fin-4	1	AY219992
13	Kolari	Fin-5	1	AY219993
14	Pajala	Swe-1	1	AY219994
15	Överkalix	Fin-Swe	1	AY219989
16	Luleå	Swe-2, Swe-3	3	AY219995, AY219996
17	Vaasa	Fin-6	1	AY219997
18	Kanin Peninsula	Rus-3, Rus-4	2	AY220001, AY220002
19	Petjora	Rus-2	1	AY220000

Table 1 Geographical information, number of specimens from each locality (N) and mtDNA haplotype designations. Figure references correspond to localities in Fig. 1

comparison, we also employed some simpler substitution models.

NJ trees were constructed in MEGA2.1 (Kumar *et al.*, 2001) and PAUP* 4.0b10 (Swofford, 1998). The outgroup consisted of a Beringian and a Central Asian root vole haplotype (AY220018 and AY220044; Brunhoff *et al.*, 2003). Bootstrap analysis was performed with 10,000 replicates. MP analyses were conducted in PAUP* using the heuristic search algorithm, 100 random or the close addition replicate, tree bisection–reconnection (TBR) swapping, the steepest descent option and three Beringian haplotypes (AY220023, AY220028 and AY220044; Brunhoff *et al.*, 2003) for outgroup rooting. Bootstrap analysis comprised 2000 replicates. The MP trees were analysed in MACCLADE 4.05 (Maddison & Maddison, 2000) and a consensus parsimony network constructed by hand. The ML tree search was conducted as described for MP but with the ‘as is’ addition replicate and the same outgroup as for the NJ analyses. Rate heterogeneity within and among lineages was evaluated by comparing log likelihood scores of ML trees constructed with and without a molecular clock constraint (Felsenstein, 1988).

Estimates of nucleotide diversity (π and θ), haplotype (h) diversity and DNA net and raw divergence (Da and Dxy) were calculated using MEGA and DNASP 3.53 (Rozas & Rozas, 1999). Standard errors (SE) were estimated by the bootstrap method using 10,000 replicates.

RESULTS

Phylogenetic analysis

The 46 individuals analysed represented 29 North European root vole cytochrome *b* haplotypes (Table 1). The 19 new

cytochrome *b* gene (1140 bp) sequences represented nine new haplotypes that have been deposited in GenBank (accession numbers DQ452134–DQ452142; Table 1). The MP, NJ and ML analyses revealed two North European sublineages labelled ‘Andøya’ and ‘Fennoscandia’. The consensus MP network and the NJ tree are presented in Fig. 2. Bootstrap support for the Andøya sublineage was estimated at 92% and 83% in the MP and NJ analyses, respectively. MP analysis did not provide support for the Fennoscandian sublineage whereas the NJ method generated 61% support. MP searches of the 37 informative sites generated two trees (CI = 0.81, 110 steps; Fig. 2a). The same NJ tree topology was obtained regardless of the substitution model employed but the highest bootstrap values were generated with the Jukes Cantor model (Fig. 2b). The ML trees constructed under a molecular clock constraint did not differ significantly from unconstrained ML trees ($\chi^2 = 29$, d.f. = 27, $P > 0.05$ without outgroup; $\chi^2 = 39$, d.f. = 30, $P > 0.05$ with outgroup).

Phylogeography and mtDNA diversity

The mtDNA sublineages had distinct geographical distributions and we therefore designate them phylogroups. The Andøya phylogroup contained root voles from the Norwegian islands of Andøya, Ringvassøya and Reinøya and the Russian localities of the Kanin Peninsula and Petjora (Figs 1 & 2). The Fennoscandian phylogroup encompassed root voles from the three Norwegian islands of Kvaløya, Håkøya and Arnøya as well as the remaining specimens from Norway, northern Sweden and Finland (Figs 1 & 2).

Nucleotide diversity within the Andøya and Fennoscandian phylogroups was similar, ranging from 0.5% to 0.7% (± 0.1 –0.2% SE) for π and from 0.6% to 0.7% (± 0.2 –0.3% SE) for θ

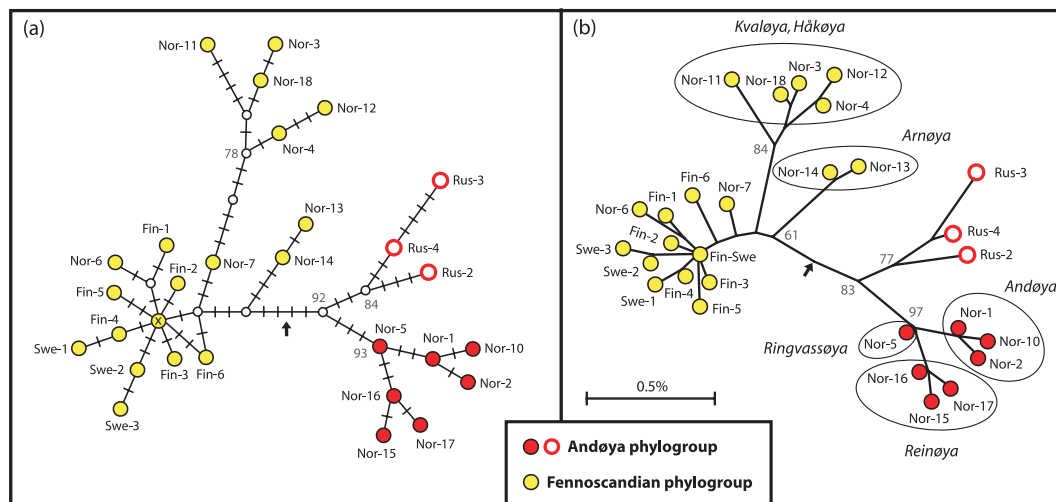


Figure 2 Phylogenetic relationships among 29 cytochrome *b* haplotypes in North European root voles (*Microtus oeconomus*). Arrows indicate the roots. (a) Consensus maximum parsimony (MP) networks of two minimal trees. Bootstrap resampling support (2000 iterations) is indicated in green. x denotes haplotype Fin-Swe. (b) Neighbour-joining (NJ) tree. Bootstrap resampling support (10,000 iterations) is indicated in green. Haplotypes from the six Norwegian islands are encircled: Andøya, Ringvassøya and Reinøya correspond to the ‘Andøya island group’ and Kvaløya, Håkøya and Arnøya to the ‘Kvaløya island group’.

Phylogroup/island group	N	No. of haplotypes	Nucleotide diversity % (\pm SE)		Haplotype diversity (h)
			π	θ	
Andøya phylogroup	12	10	0.68 (0.15)	0.61 (0.26)	0.96 (0.06)
Fennoscandian phylogroup	34	19	0.54 (0.13)	0.71 (0.24)	0.96 (0.02)
Andøya island group	9	7	0.26 (0.10)	0.26 (0.14)	0.92 (0.09)
Kvaløya island group	12	5	0.30 (0.10)	0.26 (0.13)	0.79 (0.09)
Total	46	29	0.94 (0.16)	1.06 (0.33)	0.97 (0.01)

Table 2 Estimates of mtDNA variability in North European root voles (*Microtus oeconomus*)

(Table 2). Total (raw) divergence between the phylogroups was estimated at $1.4 \pm 0.3\%$, whereas the net distance was $0.8 \pm 0.2\%$. Nucleotide diversity within two groups of Norwegian islands, the Andøya island group (Andøya, Ringvassøya and Reinøya) and the Kvaløya island group (Kvaløya, Håkøya and Arnøya), was calculated for comparison, even though the latter group does not represent a monophyletic lineage, and estimated at $0.3 \pm 0.1\%$ (Table 2). The number of haplotypes per island is given in Table 2. Almost all individuals in the Andøya island group carried unique cytochrome *b* haplotypes.

DISCUSSION

Two evolutionary lineages in northern Fennoscandia

This study shows that the North European mtDNA phylogroup (Brunhoff *et al.*, 2003) in the root vole is further divided into a Fennoscandian and an Andøya phylogroup. The Fennoscandian phylogroup is distributed throughout northern Fennoscandia with the exception of the three Norwegian islands of Andøya, Ringvassøya and Reinøya. Root voles from these three islands do not group with the geographically close islands of Kvaløya, Håkøya or Arnøya or mainland Fennoscandia (Fig. 1). Instead, they form the Andøya phylogroup that also includes specimens from north-west Russia.

A survey of Y chromosome sequence variability in the root vole indicates some congruence in mtDNA and Y chromosome phylogeographical patterns (Brunhoff, 2003; Brunhoff *et al.*, submitted). The results show that root voles from mainland Fennoscandia have identical Y chromosome haplotypes, whereas individuals from the Norwegian islands carry unique haplotypes. The single Andøya root vole analysed for Y chromosome variation carried a haplotype that is closely related to haplotypes from north-west Russia. Our mtDNA data are also in accordance with Siivonen's (1968) description of a separate morphological subspecies of root vole, *M. oeconomus finmarchicus*, on the Vesterålen Islands to which Andøya belongs. Altogether, the available data suggest that the two mtDNA phylogroups in northern Europe reflect separate populations with specific evolutionary histories (cf. Avise, 2000).

The net divergence of $0.8 \pm 0.2\%$ (SE) between the Andøya and Fennoscandian phylogroups corresponds to a separation 80,000–130,000 yr ago (95% CI = 40,000–200,000 yr ago) when using a divergence rate of 6–10% per million years

(cf. Brunhoff *et al.*, 2003). This dating suggests that the separation of the two phylogroups pre-dates the LGM at 21,000–17,000 yr BP. It may even be that this event coincides with the previous interglacial (130,000–115,000 yr ago) since it is likely that the root vole experienced a geographical range decrease during this period similar to the species' decline in central Europe during the Holocene (cf. Mitchell-Jones *et al.*, 1999; Brunhoff *et al.*, 2003).

The distribution of the Fennoscandian phylogroup most likely reflects post-glacial ($\geq 10,000$ yr BP) recolonization of northern Fennoscandia via an eastern route through Finland as described for many other organisms (Brunhoff *et al.*, 2003 and references therein). The Andøya phylogroup on the other hand may reflect glacial survival *in situ* in north-western Norway or, alternatively, late glacial colonization along the northern coasts of Russia and Norway.

Glacial survival on Andøya

Andøya island belongs to the Lofoten-Vesterålen archipelago, i.e. the group of islands that Siivonen (1968) suggested as a glacial refugium for the subspecies *M. oeconomus finmarchicus*. Our mtDNA and Y chromosome data are consistent with glacial survival of root voles on Andøya because root voles from this island, together with a few neighbouring islands, exhibit a specific evolutionary branch. Thus, contrary to genetic analyses of plants (e.g. Gabrielsen *et al.*, 1997; Tollefsrud *et al.*, 1998; Brochmann *et al.*, 2003), the root vole data indicate that genetic footprints of glacial survival *in situ* on the north-west coast of Norway have not been erased by post-glacial immigration but are possible to detect even today. The results are particularly remarkable since at least parts of Andøya were ice-free even during the LGM (Vorren *et al.*, 1988; Svendsen *et al.*, 2004), and because macrofossil findings of plants such as grasses and records of invertebrates point to an uninterrupted Late Weichselian presence of some plant species on this island (Alm & Birks, 1991; Solem & Alm, 1994).

There are, however, two factors that are somewhat difficult to reconcile with glacial survival on Andøya for root voles: past periods of cold arctic climate and the level of mtDNA diversity observed today in the Andøya island group. There were several periods with high arctic climate on Andøya between 22,000 and 12,000 yr BP (Vorren *et al.*, 1988; Alm & Willassen, 1993; Vorren & Alm, 1999). Although the current root vole range

also includes arctic biota (mainly the southern arctic bioclimatic zone), the dry glacial conditions with sparse grass vegetation may have made the island inhospitable for root voles during the coldest periods (cf. Vorren *et al.*, 1988; Alm, 1993) since the species generally requires moist to wet habitats. The establishment of *Microtus* voles beyond their normal bioclimatic range will probably require particular circumstances. For instance, the sibling vole *Microtus rossiaemeridionalis* became established in the middle arctic zone at Svalbard, 20° N of their main distribution range in Europe, evidently due to particularly benign local conditions with extremely lush bird cliff vegetation providing food resources and a well-drained substrate fulfilling this species' subterranean habits (Fredga *et al.*, 1990). Whether the extreme high arctic environment along the north Norwegian coast fulfilled basic habitat requirements for root voles to sustain populations of several thousand voles during the coldest periods of the last glaciation is very uncertain. Fossil remains show that the root vole was widely distributed in central Europe during the LGM, occurring as far north as southern Poland (Chaline, 1987; Nadachowski, 2001, personal communication), but its distribution was patchy and concentrated to periglacial areas with marsh environments (Chaline *et al.*, 1995). On the other hand, the fossil data also demonstrate that the root vole was capable of long-term survival in very small, isolated populations (Horáček, 2000) and recent findings suggest that small mammal distributions are not always explained by climatic parameters, such as temperature and precipitation, and that climate as derived from palynology should not be taken without question (Stewart *et al.*, 2003; Stewart, 2005).

The mtDNA variability in the Andøya island group is low ($\pi = 0.26\%$) but it might be considered somewhat too high to reconcile with glacial survival of a small, isolated population for thousands of years on a single island. Theoretically, we would expect a more star-like phylogeny and even lower mtDNA variation – similar to the data reported for the Norwegian lemming (*L. lemmus*), another species hypothesized to have survived the LGM in a local Scandinavian refugium (Fedorov & Stenseth, 2001). However, if there had been root vole populations surviving on several other islands except Andøya, the current pattern with one or a few closely related mtDNA haplotypes per island would represent a plausible outcome. In fact, Alm & Birks (1991) suggested that other parts of the Vesterålen-Lofoten islands could have experienced conditions similar to Andøya. Moreover, mtDNA analyses of Orkney voles (*Microtus arvalis orcadensis*) demonstrate that relatively small island populations of voles can sometimes exhibit surprisingly high levels of genetic variation (Haynes *et al.*, 2003), some of which may have been generated by non-neutral processes (Fink *et al.*, 2004). Thus, both positive selection acting in populations experiencing harsh environmental conditions (cf. Fink *et al.*, 2004) and relaxed negative selection of slightly deleterious mutations due to small effective population sizes (e.g. Woolfit & Bromham, 2005) could have contributed to mtDNA diversity. Actually, four of the eight substitutions within the Andøya island group are nonsynonymous, causing amino acid changes, and

one of them occurs in a highly conserved region of the cytochrome *b* gene (data not shown).

An alternative scenario involving late glacial colonization

Alternatively, the Andøya phylogroup may derive from an early recolonization wave of late glacial colonizers that used ice-free areas along the northern coasts of Russia and Norway in accordance with the scenario suggested for mountain reindeer (*Rangifer tarandus tarandus*; Rankama & Ukkonen, 2001). This colonization route was available thousands of years earlier than the route via Finland (cf. Eronen *et al.*, 2001; Svendsen *et al.*, 2004). According to this late glacial immigration model, the pioneering root voles may have been dispersed over larger areas initially and the current populations on Andøya, Ringvassøya and Reinøya represent relics. Periods with high arctic climate (e.g. 11,000–10,000 yr BP; Andersen & Borns, 1997), periods with dry conditions (e.g. 8900–7600 yr BP; Jensen *et al.*, 2002) and/or competition with root voles belonging to the Fennoscandian phylogroup, as well as other species, could have caused local extinctions. Competition could also explain why root voles are not found along the coastline of mainland Norway, nor on some of the larger islands in north-west Norway, even though habitats are similar to the islands where they occur today. Instead, in these areas, field voles (*Microtus agrestis*) are found in habitats that are typical for root voles (Yoccoz and Ims, unpublished data).

CONCLUSIONS

The phylogeographical patterns of North European root voles are compatible with glacial survival on Andøya. However, relatively high genetic diversity in contemporary island populations and severe climatic conditions on Andøya during the last glaciation raise question marks. An alternative scenario involving late glacial recolonization along the northern coasts of Russia and Norway combined with a subsequent, second colonization wave via north-eastern Finland can therefore be a viable alternative. More intense sampling of root voles from northern Scandinavia and western Russia using several genetic markers will be needed to solve this issue.

Theoretically, both the glacial survival and the late colonization model would imply low genetic variation, the former due to historically low effective population sizes and the latter due to loss of variation during the colonization process (cf. Nichols & Hewitt, 1994). The fact that the root vole displays much mtDNA variation in northern Norway demonstrates that these simple theoretical models do not always apply to northerly species (cf. Fedorov, 1999; Fedorov *et al.*, 1999b). Instead, complex recolonization histories involving range expansion from several glacial refugia and, possibly, several waves of colonization, combined with local, post-glacial extinctions of populations can create intricate patterns of genetic differentiation and relatively high levels of variation, as described for several other non-arctic northern small mammals (Jaarola *et al.*, 1999; Haynes *et al.*,

2003). Survival *in situ* in Scandinavian glacial refugia may represent yet another, although admittedly rare, phenomenon that has contributed to the complex patterns.

ACKNOWLEDGEMENTS

We are indebted to Alexander Dekonenko, Vadim Fedorov, Karl Fredga, Voitto Haukialmi, Heikki Henttonen and Asko Kaikusalo for providing samples. We would also like to thank Karl Fredga, Christian Hjort, Voitto Haukialmi and Adam Nadachowski for invaluable advice and discussions, and Bengt Olle Bengtsson, Natália Martinková, Helena Mattisson, Ettore Randi and John R. Stewart for comments on a previous version of the manuscript. Financial support was received from the Swedish Research Council, the Erik Philip-Sörensen Foundation, the Nilsson-Ehle Foundation and the Lindström Foundation.

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BIOSKETCHES

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Editor: Brett Riddle