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Glacial survival of the Norwegian lemming (*Lemmus lemmus*) in Scandinavia: inference from mitochondrial DNA variation

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In order to evaluate the biogeographical hypothesis that the Norwegian lemming (*Lemmus lemmus*) survived the last glacial period in some Scandinavian refugia, we examined variation in the nucleotide sequence of the mitochondrial control region (402 base pairs (bp)) and the cytochrome *b* (cyt *b*) region (633 bp) in Norwegian and Siberian (*Lemmus sibiricus*) lemmings. The phylogenetic distinction and cyt *b* divergence estimate of 1.8% between the Norwegian and Siberian lemmings suggest that their separation pre-dated the last glaciation and imply that the Norwegian lemming is probably a relic of the Pleistocene populations from Western Europe. The star-like control region phylogeny and low mitochondrial DNA diversity in the Norwegian lemming indicate a reduction in its historical effective size followed by population expansion. The average estimate of post-bottleneck time (19–21 kyr) is close to the last glacial maximum (18–22 kyr BP). Taking these findings and the fossil records into consideration, it seems likely that, after colonization of Scandinavia in the Late Pleistocene, the Norwegian lemming suffered a reduction in its population effective size and survived the last glacial maximum in some local Scandinavian refugia, as suggested by early biogeographical work.

Keywords: glaciation; glacial refugia; biogeography; phylogeography; mitochondrial DNA; bottleneck

1. INTRODUCTION

For the past 100 years, there has been considerable discussion around the issue of whether Arctic and Alpine species of the Scandinavian biota might have survived during the last glacial period in some local ice-free refugia in Scandinavia. The glacial survival hypothesis, which was initially based on biogeographical arguments for plants (Dahl 1987) and animals (Siivonen 1982), remains highly controversial. Biogeographical data alone are of limited use because they cannot be used for separating dispersal from local refugia and post-glacial colonization from periglacial areas south of the ice sheet in continental Europe. Although geological data are still insufficient, they do not generally support the glacial survival hypothesis as no positive evidence for the existence of permanent ice-free areas throughout the entire last glacial period (Weichselian, 115–10 thousand years before present (kyr BP)) (Andersen & Borns 1997) has been found in Scandinavia (Donner 1995). However, it is known that the last glacial period was repeatedly interrupted by warm interstadials (Donner 1995). Recent palaeoecological findings have indicated extensive ice-free areas during warm intervals in Scandinavia (24.5–38 kyr BP) (Valen *et al.* 1996; Ukkonen *et al.* 1999). Furthermore, palaeoecological records indicate an ice-free environment even around the last glacial maximum (18–22 kyr BP) (Andersen & Borns 1997) in north-western Norway (Alm & Birks 1991; Møller *et al.* 1992; Alm 1993).

Historical events are also recorded in the genes and gene pools of extant species. Therefore, analysis of genetic data, in particular those incorporating gene genealogies, provides insight into the historical factors generating the extant patterns of genetic variation (cf. Hewitt 1996). Recently, several genetic studies have addressed the long-standing question of possible glacial survival of various species in Scandinavia. The pattern of genetic differentiation among populations in two species of Arctic–Alpine plants *Saxifraga* suggests extensive post-glacial dispersal making it unnecessary to invoke glacial survival as an explanation for the observed pattern (Gabrielsen *et al.* 1997; Tollefsrud *et al.* 1998). However, this does not imply that plants were unable to survive the last glaciation in local Scandinavian refugia. In contrast, strong genetic differentiation among geographical groups in the freshwater amphipod *Gammarus lacustris* (Vainio & Väinölä 1992) suggests independent colonization of Scandinavia from three genetically distinct stocks including the coastal race that possibly derived from local ice-free refugia located on the continental shelf of the Norwegian Sea (Segerstråle 1954).

The Norwegian lemming (*Lemmus lemmus* Linnaeus, 1758) is the only vertebrate endemic to Scandinavia. Consequently, it has been suggested that this Arctic rodent evolved by surviving either the last glacial period or the last glacial maximum (Ekman 1922) in some local Scandinavian refugia. In order to evaluate the hypothesis of glacial survival, we examined mitochondrial DNA (mtDNA) diversity in Norwegian lemmings sampled across the range of species distributed in the Scandinavian mountains. If the Norwegian lemming survived the last glacial maximum in some local Scandinavian refugia, then we might reasonably expect that the present pattern of mtDNA diversity will reflect expansion in its historical effective population size (cf. Rogers & Jorde 1995). Alternatively, if the Norwegian lemming colonized Scandinavia after the last glacial period from periglacial areas south of the ice sheet in continental Europe, then no genetic signs of expansion in its historical effective size would be expected. At first sight, genetic consequences of

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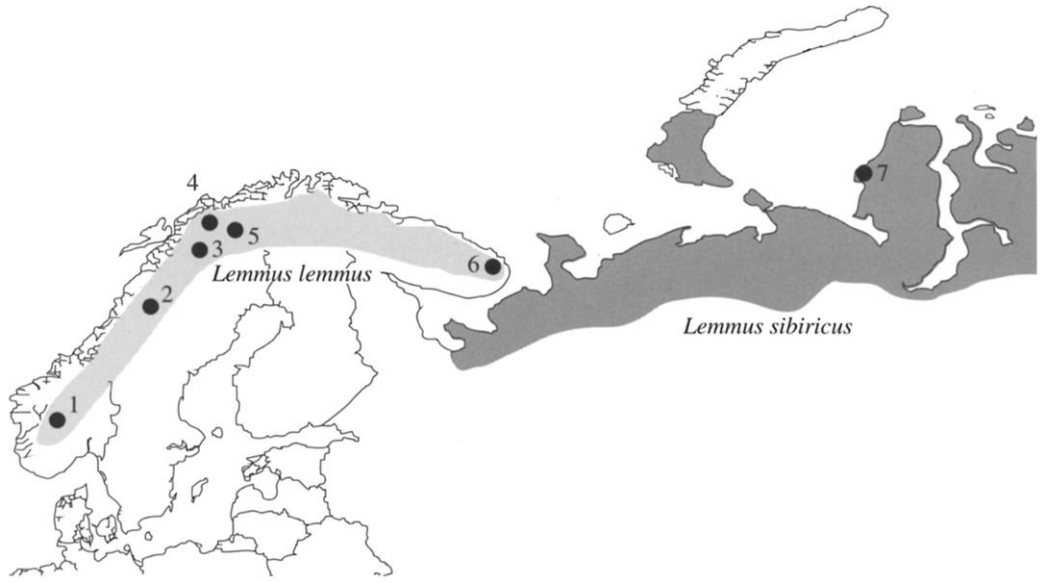

Figure 1. Map showing the sampling localities and species' ranges of distribution. For locality names refer to table 1. Only one individual was analysed from locality 6.

Table 1. *Number of lemmings sampled* (n), *number of control region haplotypes observed* (n_h), *number of variable sites* (n_s) *and haplotype* (h) *and percentage of nucleotide* (π) *diversities and their standard deviations* (*s.d.*)

locality	n	n_h	n_s	h (s.d.)	π (s.d.)
Norwegian lemming					
1. Finse	20	9	9	0.79 (0.09)	0.33 (0.07)
2. Ammarnäs	8	2	1	0.25 (0.18)	0.06 (0.05)
3. Abisko	16	7	7	0.80 (0.09)	0.39 (0.08)
4. Troms	11	5	6	0.76 (0.10)	0.37 (0.10)
5. Kilpisjärvi	16	6	6	0.68 (0.12)	0.31 (0.09)
Siberian lemming					
7. West Yamal	7	3	11	0.76 (0.12)	1.45 (0.23)

the alternative scenario might seem inconsistent with the traditional model of post-glacial colonization by successive founder events that has been proposed for temperate taxa (Hewitt 1996). However, this alternative is based on previous findings in the phylogenetically similar Siberian lemming (*Lemmus sibiricus* Kerr, 1792) across the Eurasian Arctic, where no genetic signs of post-glacial colonization were found in populations from formerly glaciated areas as compared with non-glaciated areas (Fedorov 1999; Fedorov *et al.* 1999).

2. MATERIAL AND METHODS

In 1994–1997, Norwegian lemmings (*L. lemmus*) were collected from six localities over most of the species' distribution range in Scandinavia (figure 1 and table 1). In order to obtain interspecific divergence estimates, we analysed seven specimens of the Siberian lemming (*L. sibiricus*) collected on the Swedish–Russian Tundra Ecology Expedition 94 from the western Yamal Peninsula in Siberia (Fedorov *et al.* 1999). Total genomic DNA was isolated from frozen or dry tissues by the use of the proteinase K–salt extraction method (Miller *et al.* 1988). The hypervariable fragment of the 5′-end of the mitochondrial control region (Nachmann *et al.* 1994) was amplified by the polymerase chain reaction (PCR) using the primers P (Wilkinson & Chapman 1991) and mtl6502H (Houlden *et al.* 1999).

A total of 402 base pairs (bp) of the control region were manually sequenced according to the manufacturer's specification (Sequenase Kit, Amersham Life Science, USB Corporation, Cleveland, OH, USA) in 72 individuals of the Norwegian lemming and 7 Siberian lemmings (EMBL Database accession numbers AF348371–AF348388). In order to ensure that the control region sequences were of mitochondrial origin and not nuclear copies, we sequenced the PCR products amplified from both purified mtDNA (Fedorov *et al.* 1999) and total DNA in six individuals and obtained identical results. The mitochondrial cytochrome *b* (cyt *b*) gene was amplified by the PCR and manually sequenced using a set of primers as described by Fedorov *et al.* (1999). A total of 633 bp of the cyt *b* gene were scored in three Norwegian and five Siberian lemmings (EMBL Database accession numbers AF348389–AF348392).

Nucleotide (π) and haplotype (h) diversities and their sampling variance were estimated from the control region sequences according to Nei (1987). As only one specimen was available from locality 6 (figure 1), this locality was excluded from intrapopulation diversity analysis. The following analyses

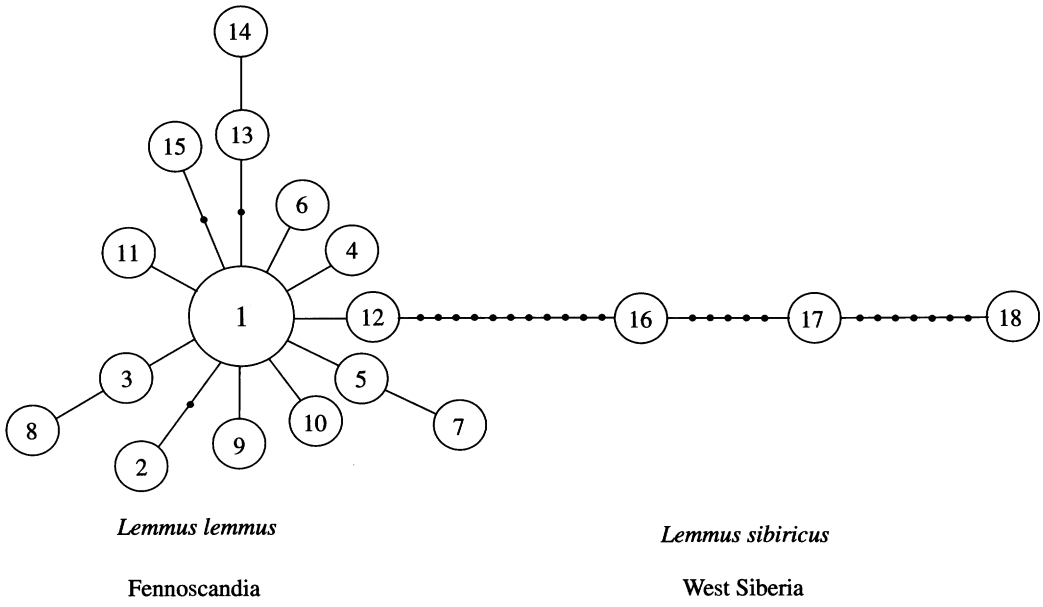

Figure 2. A minimum-spanning tree illustrating the phylogenetic relationships between 18 mtDNA control region haplotypes observed in Norwegian and Siberian lemmings. Each line between two circles corresponds to one nucleotide substitution. Filled small circles are hypothetical haplotypes that were not observed in the sample. The large circle indicates the most common (frequency 0.51) haplotype (1) in the Norwegian lemming.

of the control region variation were conducted using the program Arlequin v. 2.02 (Schneider *et al.* 2000). Phylogenetic relationships between haplotypes were inferred by a minimum-spanning tree constructed from a minimum number of pairwise site differences (Schneider *et al.* 2000). In order to measure geographical subdivisions of the control region variation among the Norwegian lemming populations, we used an analysis of molecular variance with a minimum number of mutation differences matrix as input (Excoffier *et al.* 1992). In order to infer the demographic history of the Norwegian lemming, we used two approaches. First, significance of population expansion was tested using Fu's (1997) F_s-statistics, which detect excesses of low-frequency alleles in a growing population as compared with the expected number in a stationary population. Second, we used the frequency distribution of the number of pairwise differences in the control region sequences among all individuals (the mismatch distribution) in order to estimate the initial population size of females and the timing of population expansion, both of which were expressed in units of mutational time (Rogers 1995). Parametric bootstrapping was used in order to test the observed mismatch distribution's goodness of fit to the sudden expansion model and to obtain confidence intervals around the estimated parameters (Schneider & Excoffier 1999).

The divergence rate for the control region was calibrated relative to the rate established for the cyt *b* gene. We used three Norwegian and five Siberian lemmings for which both control region and cyt *b* gene sequences were obtained. A Tamura–Nei substitution model (Tamura & Nei 1993) with a gamma distribution of mutation rates was used for estimating divergence between haplotypes. The shape parameter of the gamma distribution ($\alpha = 0.09$) was estimated from the data for the control region sequences using the maximum-likelihood approach as implemented in the PUZZLE program (Strimmer & Von Haeseler 1999). We used the shape parameter ($\alpha = 0.22$) previously estimated in voles (*Microtus*) for the cyt *b* gene sequences (Conroy & Cook 2000). Neighbour-joining trees were constructed with the MEGA program (Kumar *et al.* 1993) and the relative difference between the tree lengths was estimated.

3. RESULTS

There were 15 control region haplotypes defined by 15 variable sites among the 72 Norwegian lemmings and 3 control region haplotypes differing by 11 variable sites among the 7 Siberian lemmings. The minimum-spanning tree (figure 2) indicated a major difference between the Norwegian and Siberian lemming haplotypes. The net nucleotide divergence between the Norwegian and Siberian clades was 1.8% for the cyt *b* gene. The Norwegian lemming lineage demonstrated a star-like internal topology, with the most common (pooled frequency of 0.51) and geographically widespread haplotype (1) in the centre surrounded by rare haplotypes differing by a small number of mutational steps. The occurrence of one most common haplotype (1) in all populations of the Norwegian lemming, and low divergence between haplotypes, resulted in relatively small nucleotide diversity estimates (table 1) and a limited population structure in Scandinavia. The single specimen from locality 6 (Kola) had haplotype IV. Analysis of molecular variance showed that the amount of variation between populations was small ($\Phi_{ST} = 0.027$) and insignificantly different from zero ($p > 0.07$). Therefore, the Norwegian lemming populations, including the one specimen from locality 6 (figure 1), were pooled for diversity analyses. A significantly large negative F_s-statistic value (-9.275) ($p = 0.000$) indicated an excess of low-frequency alleles (15) as compared with the expected number (5.84) in a stationary population and provided evidence for population expansion. This inference was supported by the results of the mismatch distribution analysis (figure 3). The observed distribution of the pairwise mutation differences among Norwegian lemmings

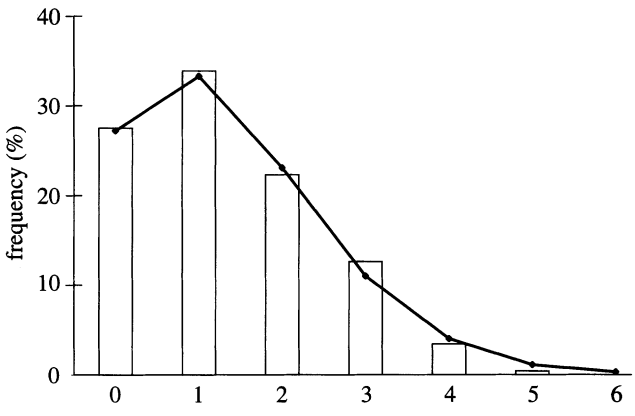

Figure 3. Distribution of the number of pairwise differences between 72 individuals of the Norwegian lemming. The numbers of pairwise differences are on the x-axis and their frequencies are on the y-axis. Bars represent the observed distribution and the line represents the expected distribution under the model of sudden expansion fitted to the data.

fitted well ($p=0.885$) with the expected distribution under a model of sudden population expansion. The low population size of females before the expansion expressed in units of mutational time ($\theta_0=0$ and 95% CI 0–1.068) suggested that the Norwegian lemming went through a bottleneck. The timing of population expansion, in this case post-bottleneck time, may be estimated by the mode of the mismatch distribution ($\tau=1.448$ and 95% CI 0.393–2.694) expressed in units of mutational time as $t=\tau/2u$, where t is the expansion time in number of generations and u is the mutation rate per generation for the whole sequence (Rogers 1995).

The precision of time-estimates depends strongly on calibration of the mutation rate for the control region, which is unknown for lemmings. The divergence rate for the control region was calibrated relative to the rate established for the cyt *b* gene. A total of 21 substitutions (20 transitions and one transversion) among the 402 bp of the control region were observed in the eight lemmings and this corresponded to the corrected estimate of 0.0901 mutations per nucleotide site along the neighbour-joining tree (not shown). There were 15 silent substitutions (13 transitions and 2 transversions) among the 633 bp of the cyt *b* gene in the same individuals and the estimated number of mutations per site along the tree was 0.0267. Thus, the control region evolved 3.4 times faster than the cyt *b* gene. The conventional divergence rate for the mammalian cyt *b* gene is 2% per million years (Myr) (Avise *et al.* 1998). However, a higher divergence rate has been suggested for the cyt *b* gene of small mammals, such as insectivores and rodents (Martin & Palumbi 1993; Lessa & Cook 1998). The first occurrence of *Lemmus* fossil records in North America suggested that vicariant separation by the Bering Strait throughout the Pleistocene (1.8 Myr ago) resulted in the cyt *b* gene divergence estimate of 9% between the Siberian lemming and the nearctic brown lemming (Fedorov *et al.* 1999). This gives a divergence rate of 5% Myr^{-1} for the cyt *b* gene and it translates to an estimate of 17% Myr^{-1} for the control region. This rate slightly exceeds other divergence rates that have been reported for the control region of small mammals, for example 8.3–14.3% Myr^{-1} in shrews (*Sorex*) (Stewart & Baker 1994) and 10% Myr^{-1} in mice (*Mus*) (Nachman *et al.* 1994). Under the control region divergence rate of 17% Myr^{-1}, the population expansion time estimated from the mode (τ) of the mismatch distribution for the Norwegian lemming is 21.14 kyr (95% CI 5.75–39.42 kyr). The average time to common ancestry in a bottlenecked population, specifically the post-bottleneck time, can also be estimated from the mean number of nucleotide differences between pairs of individuals (1.315 and 95% CI 0.631–2.263) and the mutation rate (Rogers & Jorde 1995). This gives a time-estimate of 19.24 kyr for the population expansion after the bottleneck, which is compatible with the estimate obtained from the mismatch distribution mode, but has a smaller 95% confidence interval (9.23–33.11 kyr).

4. DISCUSSION

The phylogenetic distinction and amount of divergence between Norwegian and Siberian lemmings suggest that their separation pre-dated the last glaciation (Weichselian, 115–10 kyr BP) (Andersen & Borns 1997). The net cyt *b* gene divergence estimate (1.8%) between the Norwegian lemming and the Siberian lemming from Yamal is at least two times larger than the intraspecific divergence (0.7–0.9%) between the same haplotypes from Yamal and haplotypes from distant localities in central Siberia (Fedorov 1999; Fedorov *et al.* 1999). This implies that historical separation was more important for the genetic discontinuity between the Norwegian and Siberian lemmings than isolation by distance alone. The two species of lemmings cannot be distinguished from palaeontological data (Kowalski 1995). However, Pleistocene fossil records indicate that, during the glacial periods, *Lemmus* was continuously distributed in periglacial areas of continental West Europe (Bennike *et al.* 1994; cf. Kowalski 1995) and presumably colonized Scandinavia from continental Europe during the Late Quaternary period (cf. Siivonen 1982). Consistent with this, the phylogenetic distinctiveness of the Norwegian lemming suggests that this lineage is likely to be a relic of the Pleistocene populations from Western Europe. Today, lemmings do not occur in the western part of continental Europe. Thus, it is not possible to obtain a divergence estimate from which to infer the time of separation from mainland source populations and colonization of Scandinavia by the Norwegian lemming. Nevertheless, the minimum time that lemmings have existed in Scandinavia may be approximately estimated from the present amount of mtDNA diversity in the Norwegian lemming.

The star-like phylogeny and low mtDNA diversity in the Norwegian lemming provide evidence for a past reduction in its effective size followed by population growth (Slatkin & Hudson 1991) and may be attributed to either an *in situ* bottleneck event common to all populations or a founder effect resulting from post-glacial colonization. It is worth noting that the average estimate of the post-bottleneck time is close to the last glacial maximum (18–22 kyr BP) (Andersen & Borns 1997). The first scenario implies that the Norwegian lemming went through the bottleneck and survived the last glacial maximum in a local Scandinavian refugium. There is no positive evidence

of permanent ice-free areas in Scandinavia throughout the entire Weichselian glaciation (cf. Donner 1995). However, it is known that the last glacial period was repeatedly interrupted by warm interstadials (cf. Donner 1995) and during the latest warm interval (24.5–38 kyr BP) (cf. Larsen *et al.* 1987; Valen *et al.* 1996) much of coastal Norway is known to have been ice free. Fossils of *Lemmus* dated to 30 kyr BP have been reported from the western coast of Norway during this time interval (Larsen *et al.* 1987). The fossil records of large grazing mammals such as reindeer and mammoths furthermore suggest that ice-free areas in Fennoscandia were rather extensive between 22.4 and 34.3 kyr BP (Valen *et al.* 1996; Ukkonen *et al.* 1999). Furthermore, pollen and plant macrofossil records indicate an ice-free environment around the last glacial maximum (18–22 kyr BP) in Andøya on the north-western coast of Norway (Alm & Birks 1991; Møller *et al.* 1992; Alm 1993). Taking these findings into consideration, it seems likely that, after colonization of Scandinavia in the Late Pleistocene, the Norwegian lemming suffered a reduction in effective population size and survived the last glacial maximum in a local refugium, as suggested by early biogeographical work on the history of the Arctic species of Scandinavia (cf. Siivonen 1982). Direct evidence of glacial survival in Scandinavia would be a continuous Weichselian sequence of *Lemmus* fossil records. However, the lack of such a continuous record is not unexpected if a local refugium was located on the eustatically dry continental shelf of the Norwegian Sea (Segerstråle 1954), which was submerged after the last glaciation.

An alternative explanation for the star-like phylogeny and low mtDNA diversity in the Norwegian lemming is a reduction in its historical effective size resulting from post-glacial colonization of Scandinavia by a limited number of founders from periglacial areas in continental Europe. Low genetic diversity in populations from formerly glaciated areas (Sage & Wolff 1986) is commonly attributed to successive founder events during post-glacial colonization (cf. Hewitt 1996). However, the model of post-glacial colonization by successive founder events was proposed for temperate taxa (cf. Hewitt 1996) with the exception of cold-tolerant Arctic terrestrial species (Taberlet *et al.* 1998). Similar to other species (cf. Jaarola *et al.* 1999), the Norwegian lemming might have recolonized newly available habitats in Scandinavia from continental Europe following the glacial retreat between 9 and 14 kyr BP. We cannot reject such a scenario on the basis of our time-estimates because the period of deglaciation is within the confidence limits for the estimate of post-bottleneck time in the Norwegian lemming. However, in contrast to the Norwegian lemming, neither any decrease in mtDNA diversity nor any signs of expansion in its historical effective size were reported for populations of the Siberian lemming from areas glaciated during the Weichselian glaciation as compared with non-glaciated areas across the Eurasian Arctic (Fedorov 1999; Fedorov *et al.* 1999). These previous findings imply that range expansion of periglacial populations without a reduction in their historical effective size rather than successive founder events was a common dispersal strategy for post-glacial colonization by Arctic lemmings. There is no reason to assume a different colonization mode for Scandinavia where a high level of mtDNA diversity was reported in several species of rodents, which were early post-glacial immigrants (cf. Jaarola *et al.* 1999). Thus, founder events during post-glacial colonization seem not to be a likely explanation for the star-like phylogeny and low mtDNA diversity in the Norwegian lemming. Consistent with this, there is no support for post-glacial colonization of Scandinavia by the Norwegian lemming from the fossil records available to date. While fossils of *Lemmus* have been recorded from the periglacial area in Denmark before the last glacial maximum (Bennike *et al.* 1994), lemmings are lacking in the Danish small mammal fauna (11.5 kyr BP) (Aaris-Sørensen 1995) during the time of post-glacial colonization of Scandinavia by mammals from the south via a land bridge (cf. Jaarola *et al.* 1999).

The findings of this study support the biogeographical hypothesis (cf. Siivonen 1982) that the Norwegian lemming survived the last glacial maximum in some local Scandinavian refugium. These results, together with recent palaeoecological and phylogeographical findings, prompt re-examination of Late Quaternary biotic history in Scandinavia.

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