Phylogeography of lemmings (*Lemmus*): no evidence for postglacial colonization of Arctic from the Beringian refugium

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Abstract

Beringia is considered as an important glacial refugium that served as the main source for colonization of formerly glaciated Arctic regions. To obtain high resolution views of Arctic refugial history, we examined mitochondrial cytochrome *b* phylogeography in the northern genus of rodents, *Lemmus* (true lemmings), sampled across its circumpolar distribution. Strong phylogeographical structure suggests vicariant separation over several glacial–interglacial periods and does not provide evidence supporting the importance of Beringia for extensive colonization of formerly glaciated regions. Rather than a source of postglacial colonization, Beringia represents an area of intraspecific endemism previously undetected by biogeographical analysis. Existing phylogeographical structure suggests that vicariant separation by glacial barriers was an important factor generating genetic divergence and, thus, increasing genetic diversity in lemmings on continental and circumpolar scales. However, there is little evidence for the direct effect of the last glaciation on the level of genetic variation and allele genealogy in lemmings on a regional geographical scale. This finding implies that the population genetic models of postglacial colonization suggested for temperate taxa might have limited applicability for Arctic species.

Keywords: Alaska, biogeography, cytochrome *b* gene, genetic variation, mitochondrial DNA

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Introduction

Alternating glacial and interglacial periods during the Quaternary had a strong influence on the distribution and diversity of Arctic species (Pielou 1991). From a circumpolar perspective, an important historical event for Arctic biota was the existence of the Bering Land Bridge connecting Eurasia and North America. Due to lowering of the sea level during the glacial periods, the exposed continental shelf in combination with ice-free mainland between the Kolyma River in northeastern Siberia and the Mackenzie River in northwestern Canada formed a single nonglaciated land, Beringia. Apart from its importance for the transcontinental migration of plants and animals, Beringia is considered as an important glacial refugium

that served as the main source for multiple recolonizations of subsequently deglaciated regions in the Arctic (Hultén 1937; Pielou 1991; Elias *et al*. 2000). This traditional view of Beringia is based on biogeographical arguments derived from the Holarctic distribution of a number of morphologically defined species. However, biogeographical approaches using currently recognized species as units of analysis have relatively low resolution for inferring the historical processes of the Quaternary glacial–interglacial periods (Riddle & Hafner 1999). High resolution views of refugial and colonization history are possible through phylogeography, the analysis of the geographical distribution of genealogically related alleles (Avise 2000).

Recent advances in geology and palaeontology do not support the proposition that the Beringian refugium was a primary source for postglacial colonization of the Eurasian Arctic. The extent of the last glaciation (115–10 thousand

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years before present (kyr)) was limited in Eurasia (Andersen & Borns 1997; Svendsen *et al.* 1999). Furthermore, fossil records show that during the glacial periods in Eurasia, Arctic species expanded their distribution ranges thousands of kilometres to the south (Markova *et al.* 1995). In line with these findings, strong mitochondrial DNA (mtDNA) phylogeographical structure across the Eurasian Arctic in the two genera of lemmings *Dicrostonyx* and *Lemmus* (Fedorov *et al.* 1999a,b) and the dunlin *Calidris alpina* (Wenink *et al.* 1996; Wennerberg 2001) implies vicariant separation during several glacial–interglacial periods and provides little evidence for colonization events from a Beringian source.

In contrast to Eurasia, the North American Arctic was glaciated extensively during the Pleistocene glacial periods (Andersen & Borns 1997). Biogeographical and palaeontological evidence suggest that Beringia represented an important glacial refugium and the main source of postglacial colonization in the North American Arctic (Hultén 1937; Pielou 1991). However, Arctic species might also have survived in periglacial areas to the south of the Pleistocene ice sheets (Pielou 1991). The relative importance of the Beringian and southern periglacial refugia for postglacial colonization of North America by terrestrial taxa remains unclear.

We examine mtDNA phylogeography in the northern genus of arvicoline rodents, *Lemmus* (true lemmings), across its circumpolar distribution. On the basis of geographical distribution of morphologically defined subspecies, Macpherson (1965) suggested that lemmings colonized deglaciated areas in the North American Arctic from Beringia. However, sparse fossil records indicate that, during the glacial periods, lemmings also occurred to the south of the Pleistocene ice sheets (Burns 1980).

Two historical scenarios, postglacial colonization of the North American Arctic from a single Beringian refugium vs. colonization from Beringia and the southern periglacial areas, produce alternative predictions that may be tested by examination of mtDNA phylogeography. Under the first scenario, only mtDNA lineages related closely to the Beringian lineages are expected to occur in deglaciated areas of the North American Arctic. Alternatively, distinct phylogeographical groups deriving from the separate Beringian and southern refugia are expected within the species distribution range in North America. In order to evaluate these two scenarios of postglacial colonization, this study focuses on phylogeography of lemmings from the North American Arctic. We include data from the Eurasian Arctic in order to compare timing of the main vicariant events across the two continents with the extent of the Pleistocene glaciations.

We also examine and compare genetic footprints of demographic history in lemmings from ice-free Beringia vs. extensively glaciated regions of the North American

Fig. 1 Map showing the sampling localities, geographical ranges of the closely related species: *Lemmus lemmus*, *L. sibiricus*, *L. trimucronatus*, and the geographical distribution of mtDNA phylogeographical groups: W, Western group; C, Central group; B, Beringian group; and E, Eastern group. Geographical range of distribution of the Beringian group covers Beringia. The western limit of distribution of the Eastern group approximately corresponds to the western limit of the ice sheets during the last glaciation. Localities are designated as haplotypes in Fig. 2.

Arctic to evaluate applicability of existing population genetic models of colonization for Arctic species.

Materials and methods

Although the taxonomy of true lemmings is controversial, we follow Jarrell & Fredga (1993) in regarding *Lemmus* from Arctic as three closely related species (Fig. 1): *L. lemmus* on the Scandinavian Peninsula, *L. sibiricus* in the Eurasian Arctic and *L. trimucronatus* in northeastern Siberia and North America. These species interbreed in captivity (cf. Jarrell & Fredga 1993), so we use phylogeographical groups rather than species as units of analysis in this study. Our sampling strategy was to maximize the number of localities sampled across the distribution of the genus. In order to examine phylogeographical structure on a circumpolar scale, one to three individuals were studied from each locality. We examined a total of 40 lemmings from 31 localities (Fig. 1). In Eurasia, lemmings were collected during the summer of 1994 on the Swedish–Russian Tundra Ecology Expedition. Specimens from Alaska were obtained from the Alaska Frozen Tissue

Collection, University of Alaska Museum. Lemmings were collected from the three Canadian localities (23, 27, 28) on the Swedish Tundra Northwest Expedition in summer 1999. Additional specimens from the Canadian Arctic (localities 29, 30, 31) were obtained from the Division of Zoology, University of Oslo. Sequences (EMBL database Accession nos AJ012671–AJ012678) from some localities in Eurasia (1–12) and Alaska (20) have been published elsewhere (Fedorov *et al.* 1999b).

Total genomic DNA was isolated from frozen or ethanol preserved tissue samples by the use of the proteinase K-salt extraction (Miller *et al.* 1988) or the Qiagen tissue kit. The 915 base pair (bp) segment of the mitochondrial cytochrome *b* gene was amplified by the polymerase chain reaction (PCR) and sequenced manually or automatically using several pairs of primers, as described elsewhere (Fedorov *et al.* 1999b). A total of 827 bp of the cytochrome *b* gene were scored in all individuals (EMBL database Accession nos AY219140–AY219171).

Maximum likelihood and neighbour-joining phylogenetic reconstructions were performed using the computer program PAUP* version 4.0 (Swofford 2000). We used a test based on the minimum theoretical information criterion (AIC) implemented in the computer program MODELTEST (Posada & Crandall 1998) to select the simplest nucleotide substitution model with good fit to the data. Average nucleotide divergence within phylogeographical groups, net divergence between groups and their standard deviations were estimated according to Nei & Kumar (2000). We compared the log likelihood scores of trees constructed with and without a molecular clock assumption (Felsenstein 1988) to evaluate constancy in rates of cytochrome *b* evolution among lineages. In order to assess approximate timing of historical events, we used the divergence rate of 5% per million years (myr) as suggested previously for the cytochrome *b* region on the basis of *Lemmus* fossil records (Fedorov & Stenseth 2001).

To infer the demographic history of phylogeographical groups in the North American Arctic, we used two approaches. First, significance of population expansion or decline was tested using likelihood estimation by the Metropolis–Hasting sampling algorithm as implemented in FLUCTUATE version 1.3 (Kuhner *et al.* 1998). This method is most sensitive to demographic changes because it incorporates information from allele genealogy not used in other tests (Kuhner *et al.* 1998). The method estimates the goodness-of-fit of a model of exponential growth or decline, and generates maximum-likelihood estimates of the growth parameter (g) and its standard deviation. Positive values of g indicate demographic growth, negative values indicate decline. Because estimates of the growth rate may be biased upwards (Kuhner *et al.* 1998), we have conservatively used 99.9% confidence intervals for g to test significance of difference from zero. Second, if significant

demographic expansion had been detected by the likelihood method, we used the frequency distribution of the number of pairwise differences among haplotypes (the mismatch distribution approach) to estimate timing of population expansion (Rogers 1995). Parametric bootstrapping as implemented in ARLEQUIN (Schneider *et al.* 2000) 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).

Results

Phylogeographical structure

There were 40 different cytochrome *b* haplotypes defined by 172 variable sites among the 40 lemmings. The smallest values of the minimum theoretical information criterion (AIC = 6392.7075) indicated that the Tamura & Nei (1993) substitution model with proportion of invariable sites ($I = 0.6293$) and gamma distribution of mutation rates ($\alpha = 0.8808$) was the simplest model that provided good fit for the cytochrome *b* sequences. Although only the neighbour-joining tree is shown (Fig. 2), maximum likelihood searches produced the same relationships among major lineages. The tree (Fig. 2) shows the main phylogenetic division (net divergence of 7.9 ± 1% (SE)) across the Kolyma River that represents the western border of Beringia (Fig. 1). The Beringian phylogroup includes haplotypes from both sides of the Bering Strait. In Eurasia, there is a second phylogenetic division across the Lena River (3.8 ± 0.6%) that defines the Western and Central phylogroups. In North America, the main phylogenetic split (5.2 ± 0.8%) separating the Beringian and Eastern phylogroups is across the Mackenzie River on the north (Fig. 1). These two phylogeographical groups form a contact zone in Yukon–Charley (26) and Wrangel–St Elias (25) National Parks of eastern Alaska. Thus, geographical distribution of the Beringian phylogroup is limited to the Beringian refugium. The distribution range of the Eastern lineage covers the formerly glaciated part of the North American Arctic.

The comparison of the likelihood scores of trees constructed with and without molecular clock assumption shows that the cytochrome *b* sequences have evolved at roughly constant rates ($P > 0.05$). Therefore, variation in the cytochrome *b* gene is suitable for approximate dating of historical events. The net divergence estimate between the Western and Central phylogroups in Eurasia did not differ from the divergence estimate between the Beringian and Eastern phylogroups in North America (two-tailed Student's *t*-test $P > 0.05$). Under the divergence rate of 5% per myr for the cytochrome *b* gene, the net divergence estimates among the main phylogeographical groups suggest
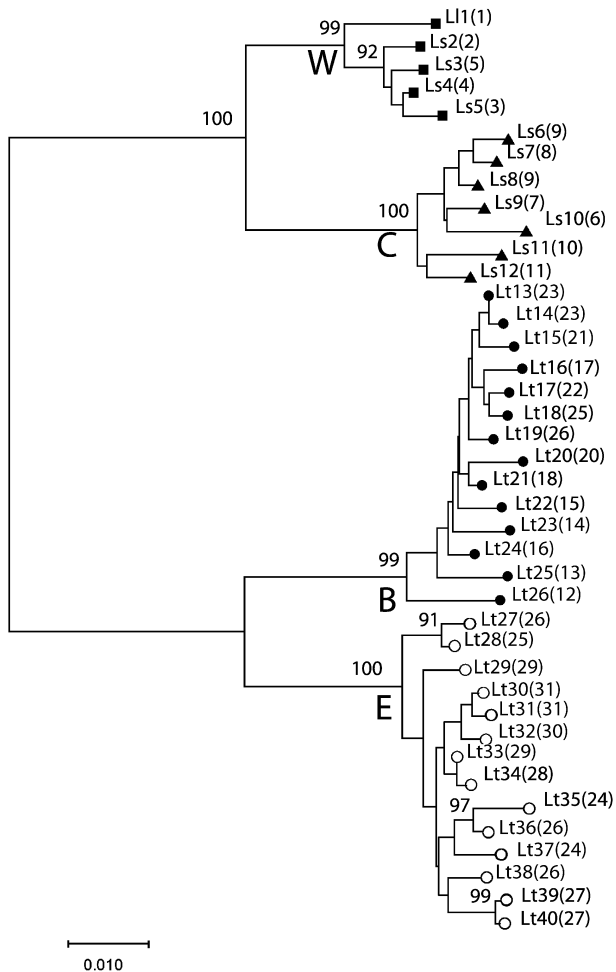
Fig. 2 Neighbour-joining tree of 40 lemming mtDNA cytochrome *b* haplotypes. Haplotypes of *Lemmus lemmus*, *L. sibiricus* and *L. trimucronatus* are designated as Ll, Ls and Lt. The four major clades are designated as in Fig. 1. Bootstrap percentages with values greater than 90% are shown for nodes. Locality numbers are in parentheses and refer to Fig. 1.

that phylogenetic divisions on both continents resulted from vicariant separation for about 0.7–1 myr.

Demographic history of North American lemmings

Analysis of the demographic history of the Eastern group from the formerly glaciated part of the North American Arctic showed clear signs of demographic expansion. Estimate of the exponential growth rate ($g = 675.24$ and 99.9% CI 378.44–972.04) significantly exceeds zero. Notably, the Beringian phylogroup in the former ice-free refugium also showed significant signs of demographic expansion ($g = 615.67$ and 99.9% CI 377.24–854.10). Similarity between the estimates of exponential growth rate indicates that, regardless of differences in glaciation history, the Eastern and Beringian phylogroups have had similar

demographic histories. It should be noted that the likelihood estimation by Metropolis–Hasting sampling is designed to infer demographic history of undivided population (Emerson *et al.* 2001) and this assumption is not met here. However, no strong phylogeographical structure was detected within either Beringian or Eastern lineages (Fig. 2), a pattern consistent with a history of expansion from a reduced source.

Inference from the likelihood method was supported by results of the mismatch distribution analysis. Observed distributions of the pairwise mutation differences among haplotypes within the Beringian and Eastern phylogroups fit ($P = 0.68$ and $P = 0.33$, respectively) the expected distribution under a model of sudden population expansion. The timing of demographic expansion may be estimated by the mode of the mismatch distribution τ 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 estimate of τ (6.680 and 95% CI 2.60–12.672) for the Beringian phylogroup was not significantly different from the estimate ($\tau = 10.431$ and 95% CI 5.841–15.773) for the Eastern group. Using the divergence rate of 5% per myr, the demographic expansion time can be estimated as 163 kyr (95% CI 63–309 kyr) for the Beringian phylogroup, and that is similar to the estimate (254 kyr and 95% CI 142–385 kyr) for the Eastern group.

The similarity in demographic history of the Beringian and Eastern phylogroups was supported further by comparison of intragroup divergence estimates. When phylogeographical structure within a group is limited, the mean intragroup divergence estimate reflects historical population size (cf. Rogers & Jorde 1995). The mean nucleotide divergence estimate within the Beringian phylogroup is identical to the mean divergence ($1.2 \pm 0.2\%$) within the Eastern lineage. The similarity between the divergence estimates suggests similar historical effective population size in the Beringian and Eastern phylogroups despite contrasting glaciation histories within their respective distributions.

Discussion

Phylogeographic structure and refugial history

Strong phylogeographic structure characterizes the circumpolar distribution of lemmings. Four distinct phylogeographical groups occur in the Holarctic and suggest vicariant separation followed by colonization of deglaciated areas in the Arctic from refugia other than just Beringia. Notably, haplotypes from Beringia represent a distinct phylogroup distributed on both sides of the Bering Strait.

Phylogeographic structure across the Eurasian Arctic is consistent with previous results based on a smaller data set

(Fedorov *et al.* 1999b). Comparative phylogeographic analyses implied that the main split in mtDNA phylogeny had resulted initially from vicariant separation by intermittent inundation of the Bering Strait and moved to the Kolyma River in the course of westward range expansion from Alaska along the Bering Land Bridge in the late Pleistocene (Fedorov *et al.* 1999b). More extensive sampling in Asian Beringia is needed to further evaluate this scenario. However, clear signs of demographic expansion and the lack of phylogeographical structure within the Beringian phylogroup support the proposal of major distributional changes that have occurred relatively recently in Beringia. In Eurasia, the second division separating the Western and Central phylogroups is observed at the Lena River. Although the extent of the Pleistocene glaciations was limited in this part of Arctic, an ice sheet on the Verkhoyansky Mountain Ridge (Andersen & Borns 1997) might be the cause of the historical barrier at the Lena. The divergence estimate of 3.8% across the river suggests that vicariant separation was initiated prior to the last glaciation (115–10 kyr, Andersen & Borns 1997). Thus, phylogeography of Eurasian lemmings implies vicariant separation during several glacial–interglacial periods and gives no evidence for colonization events from Beringia.

The division of lemmings into the Beringian and Eastern phylogroups suggests vicariant separation followed by colonization of deglaciated areas in the North American Arctic from glacial refugia other than Beringia. Similar to the Eurasian phylogroups, the divergence estimate of 5.2% between the Beringian and Eastern phylogroups implies that vicariant separation was initiated prior to the last glaciation. The similarity of divergence estimates among the phylogroups within the circumpolar range of lemmings probably indicates temporal congruence in the history of vicariance between the two continents. Approximate time estimates suggest that, on a circumpolar scale, vicariant events might have been initiated by the global change towards larger ice volumes during glacial periods at 900 kyr (Andersen & Borns 1997).

It has been shown for the collared lemming (*Dicrostonyx groenlandicus*) that some glacial refugia and important sources of postglacial colonization were located to the northwest of the main ice sheet in the Canadian Arctic (Fedorov & Stenseth 2002). However, following Macpherson (1965) we consider it unlikely that *Lemmus* could survive in glacial refugia located in the Canadian Arctic because even today, *Lemmus* does not occur in the north part of the Canadian Arctic Archipelago (Fig. 1). The present phylogeographical structure in the North American Arctic has likely resulted from colonization of the formerly glaciated areas by migrants from periglacial areas located to the south of the Pleistocene ice sheets. Palaeontology provides an independent line of evidence supporting the proposal of colonization from the south. Fossils of lemmings are sparse to the south of Beringia (Repenning 2001), but Pleistocene fossils have been recorded from three southern localities (Burns 1980; Foley & Raue 1987; Karrow *et al.* 1997). Fossils of lemmings dated prior to the last glacial maximum (18 kyr) were also reported from the Alexander Archipelago and suggest the possible existence of a coastal ice age refugium (Heaton *et al.* 1996). Taken together, phylogeographical and palaeontological data indicate that after the last glaciation lemmings colonized deglaciated areas in the North American Arctic from southern periglacial refugia. The relatively limited importance of the Beringian refugium for postglacial colonization of North America is also supported by phylogeographical congruence across several codistributed mammalian species studied to date. Consistent with this, phylogeographical structure in North American collared lemmings, *Dicrostonyx*, provides no support for colonization events from Beringia, but implies postglacial colonization from the southern and Canadian Arctic refugia (Fedorov & Goropashnaya 1999; Fedorov & Stenseth 2002). Similar to *Lemmus*, the geographical distribution of the two divergent (3.5 ± 0.2%) mtDNA lineages of the ermine, *Mustela erminea,* along with its fossil record and morphological differences, suggest that a southern refugium was a main source of postglacial colonization of the deglaciated high latitudes (Fleming & Cook 2002). In addition, both ermine and lemmings share a region of contact between their distinctive lineages (roughly the Yukon/Alaska border).

Demographic history of North American lemmings

This study reveals high similarity in the demographic history of the Beringian and Eastern phylogroups despite the contrasting glaciation history of those regions. Both lineages demonstrate similar levels of mtDNA diversity and clear signs of demographic expansion that probably started long before the beginning of postglacial colonization following the last ice retreat at 14 kyr (Andersen & Borns 1997). At first sight, these findings might seem inconsistent with the models of postglacial colonization by successive founder events (cf. Hewitt 1996) and demographic expansion from reduced refugial populations (Lessa *et al.* submitted). The first model predicts decrease in genetic diversity in populations from formerly glaciated areas compared to nonglaciated areas (Hewitt 1996). Low genetic diversity reflects decrease in historical effective size due to repeated founder events during the postglacial colonization. This model has been supported by empirical studies in a number of temperate taxa (Hewitt 1996). An expectation of the second model is that the gene pools of species that now occupy formerly glaciated areas will reflect signs of population growth due to range expansion from refugial areas during postglacial colonization (Lessa *et al.* submitted). Consistent with this expectation, genetic

signs of demographic expansion were reported in several species of boreal mammals in North America (Lessa *et al.* submitted; Conroy & Cook 2000). However, it should be noted that these models were evaluated on a number of boreal and temperate taxa and excluded the cold-tolerant, Arctic terrestrial species. In contrast to many boreal and temperate species, neither a decrease in mtDNA diversity, nor any signs of sudden expansion in historical effective size were reported for populations of lemmings from formerly glaciated areas compared with nonglaciated areas across the Eurasian Arctic (Fedorov 1999; Fedorov *et al.* 1999b). Consistent with previous findings, no genetic signs of difference in demographic history reflecting postglacial colonization are reported here between the Eastern lineage from the extensively glaciated part of the North American Arctic and the phylogroup from ice-free Beringia. Thus, results of the two independent replicates from different continents imply that distributional shift of periglacial populations without a reduction or sudden expansion in their historical effective size was a common strategy for postglacial colonization by lemmings.

Genetic signs of demographic expansion that started prior to the last glaciation imply that the Beringian and Eastern phylogroups have experienced similar demographic events in deep history. Confidence intervals for the approximate time estimates of demographic expansion include the period of ice retreat (from about 150 kyr) after the more extensive previous glaciation (Illinoian; Andersen & Borns 1997). While palaeoenvironments of the southern periglacial areas are not well known, increasing palaeoecological evidence indicates arid and cold environments during glacial periods in Beringia (cf. Guthrie 2001). Palaeontological and ecological data suggest that true lemmings are associated strongly with wet and mesic environments (Kowalski 1995; cf. Rodgers & Lewis 1986). Thus, it is reasonable to assume that a change towards more arid environment during the extensive previous glaciation would have contracted the distribution and reduced long-term effective size of lemmings in Beringia. The reduction of historical population size was followed by demographic expansion due to amelioration of environment after the previous glaciation. This idea can be tested by exploring genetic signals of demographic expansion with a similar timing in other Beringian species associated with wet and mesic environments.

Conclusions

In contrast to the traditional view (Hultén 1937; Pielou 1991), our findings do not provide evidence supporting the importance of Beringia for extensive colonization of formerly glaciated Arctic regions. Rather than sources of postglacial colonization, Beringia represents an area of intraspecific endemism previously undetected by biogeographical analysis in Arctic lemmings. Existing phylogeographical structure suggests that vicariant separation by glacial barriers was an important factor generating genetic divergence and, thus, increasing genetic diversity in Arctic lemmings on continental and circumpolar scales. However, there is little evidence for the direct effect of the last glaciation on the level of genetic variation and allele genealogy in lemmings on a regional geographical scale. This finding implies that the population genetic models of postglacial colonization developed for temperate taxa might have limited applicability for Arctic species.

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