THE ROYAL SOCIETY

Received 21 May 2002
Accepted 2 July 2002
Published online 18 September 2002

Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx groenlandicus*)

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Cryptic northern refugia beyond the ice limit of the Pleistocene glaciations may have had significant influence on the current pattern of biodiversity in Arctic regions. In order to evaluate whether northern glacial refugia existed in the Canadian Arctic, we examined mitochondrial DNA phylogeography in the northernmost species of rodents, the collared lemming (*Dicrostonyx groenlandicus*) sampled across its range of distribution in the North American Arctic and Greenland. The division of the collared lemming into the Canadian Arctic and eastern Beringia phylogroups does not support postglacial colonization of the North American Arctic from a single eastern Beringia refugium. Rather, the phylogeographical structure and sparse fossil records indicate that, during the last glaciation, some biologically significant refugia and important sources of postglacial colonization were located to the northwest of the main ice sheet in the Canadian Arctic.

Keywords: Beringia; bottleneck; biogeography; colonization; mitochondrial DNA variation

1. INTRODUCTION

Quaternary glacial–interglacial periods had a strong influence on distribution and diversity of extant species (Bennett 1997). Climatic changes associated with glacial periods have restricted species distribution ranges into refugial areas. European temperate species have been known to survive glacial periods in distant southern peninsular and eastern refugia (Hewitt 1999). However, it is suggested that the southern and eastern refugia for temperate biota were supplemented by cryptic refugia in northern Europe during the Late Pleistocene (Stewart & Lister 2001). While refugial history has been studied in temperate regions (Hewitt 2000; Willis & Whittaker 2000), Arctic species have received much less attention. Cryptic northern refugia beyond the ice limit of the Pleistocene glaciations may have had significant influence on the current pattern of biodiversity in Arctic regions (Fedorov & Stenseth 2001).

Biogeographical and palaeoecological evidence suggest that eastern Beringia—ice-free land to the west of the Mackenzie River—represented an important refugium during ice ages in the extensively glaciated North American Arctic (Hultén 1937; Pielou 1991). However, Arctic species might also have survived in some local ice-free areas to the northwest of the ice sheet in the Canadian Arctic and/or northern Greenland. The proposal of northern glacial refugia in the Canadian Arctic is based on biogeographical arguments for plants (Simmons 1913; Brassard 1970) and animals (Macpherson 1965). The fossil evidence supporting this hypothesis is sparse (Harington 1990). Thus, biological significance of non-glaciated areas in the Canadian Arctic remains unclear.

Past isolation in separate glacial refugia is reflected in divergence among genes and gene pools of extant species (Hewitt 1996). Recently, several genetic studies have addressed the question of possible glacial refugia in the Canadian Arctic. The geographical patterns of genetic differentiation in the rock ptarmigan *Lagopus mutus* (Holder *et al.* 1999) and two species of Arctic plants—*Dryas integrifolia* (Tremblay & Schoen 1999) and *Saxifraga oppositifolia* (Abbott *et al.* 2000)—are compatible with the existence of glacial refugia in the Canadian Arctic. However, an alternative explanation invoking postglacial colonization of the Canadian Arctic Archipelago from eastern Beringia cannot be excluded by these results. Phylogeographical analysis of a fast-evolving cytoplasmic marker such as animal mitochondrial DNA (mtDNA) is needed to evaluate the proposal of glacial refugia in the Canadian Arctic. The genetic signal of the past refugial separation may be stronger in species with limited dispersal. Small terrestrial mammals satisfy these conditions as nearly all rodents studied to date exhibit strong mtDNA phylogeographical structure (Avise 2000).

Here, we examine mtDNA variation in the northernmost species of rodents, the collared lemming (*Dicrostonyx groenlandicus*) sampled across its entire range of distribution in the North American Arctic and Greenland. On the basis of the geographical distribution of morphologically defined subspecies, Macpherson (1965) suggested that the collared lemming survived the last glaciation in two separate refugial areas: (i) eastern Beringia and (ii) non-glaciated parts of the Canadian Arctic Archipelago or/and north Greenland. Two historical scenarios, isolation in several glacial refugia including eastern Beringia and some ice-free areas in the Canadian Arctic, versus postglacial colonization of the Canadian Arctic from a single eastern Beringia refugium produce alternative predictions that may be tested by examination of mtDNA phylogeography. If there has been sufficient time for divergence, distinct phylogeographical groups deriving from separate refugia are expected within the species distri-

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bution range in the Canadian Arctic, Greenland and eastern Beringia. Alternatively, no phylogeographical structure (except for possible population differentiation in haplotype frequencies) is expected under the scenario of recent postglacial colonization of the Canadian Arctic from a single eastern Beringia refugium.

2. MATERIAL AND METHODS

Low mtDNA diversity has previously been found within populations of collared lemmings, *Dicrostonyx* (Fedorov & Goropashnaya 1999; Ehrich *et al.* 2000). Therefore, in order to examine phylogeographical structure on a continental scale only one or two individuals were studied from each locality. We examined a total of 47 collared lemmings from 29 localities in the North American Arctic (figure 1*a*). Lemmings were collected from 12 localities (localities 7, 10, 11, 12, 16, 17, 18, 20, 21, 23, 24 and 26) during the summer of 1999 on the Swedish Tundra North West Expedition. Specimens from Alaska and Canada (localities 2, 3, 5 and 13) were also obtained from the Frozen Tissue Collection, University of Alaska Museum. Finally, museum skins from the four high Arctic localities (localities 22, 25, 27 and 28) were provided by the Canadian Museum of Nature. Sequences from some localities in eastern Beringia (localities 1, 4, 6 and 8) and the Canadian Arctic (localities 9, 14, 15, 19 and 29) were published elsewhere (Fedorov & Goropashnaya 1999; Ehrich *et al.* 2000).

Total genomic DNA was isolated from frozen, ethanol preserved or dry tissue samples by the use of the proteinase K–salt extraction (Miller *et al.* 1988). The segment (915 bp) of the cytochrome *b* gene and 300 bp from the 5′-end of the control region were amplified by PCR and manually sequenced using several sets of primers as described elsewhere (Fedorov & Goropashnaya 1999; Ehrich *et al.* 2000). We amplified the same part of the cytochrome *b* gene from the museum skin DNA samples in four overlapping segments using AmpliTaq Gold (Perkin–Elmer) and specially designed pairs of primers: D1L, TGAAACTTGAAACATAGGCAT-3′ and D1H, TGTTAGA GAGCCTGTTTCGTGAA-3′ (280 bp); D2L, TGAAATT TCGGCTCCCTACT-3′ and D2H, GCACATACCCTAT GAATGCT-3′ (307 bp); D3L, TCTACCCTTCATCATTA CAGC-3′ and D3H, AGATCGTAAAATGGCGTAGGC-3′ (297 bp); D6L, CCACCCCTATTACACAATCA-3′ and D6H, GAATGTTAGGCCTCGTTGTT-3′ (272 bp). The same primers were used for sequencing of PCR-amplified segments. Excluding missing sites, we scored a total of 873 bp of the cytochrome *b* gene and 250 bp of the control region.

Maximum-likelihood and parsimony analyses were performed using the computer program PAUP v. 4.0 (Swofford 2000). We used a test based on the minimum theoretical information criterion implemented in the computer program ModelTest (Posada & Crandall 1998) to select the simplest nucleotide substitution model with good fit to the data. Neighbour-joining phylogenetic trees were constructed using the computer program Mega v. 2.0 (Kumar *et al.* 2001). Nucleotide diversity and divergence (net divergence) between phylogenetic groups with correction for intragroup diversity were estimated according to Nei & Kumar (2000). In order to infer the demographic history of phylogeographical groups, we tested the significance of population expansion or decline by the use of likelihood estimation by the Metropolis–Hasting sampling algorithm as implemented in Fluctuate v. 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 growth and 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 (CIs) for g to test significance of difference from zero.

3. RESULTS

There were 34 different cytochrome *b* haplotypes defined by 65 variable sites among the 47 collared lemmings. In order to increase phylogenetic resolution we included an additional subset of data into our analysis containing the 34 control region sequences for lemmings with different cytochrome *b* haplotypes. A total of 81 sites were variable in the dataset combining the cytochrome *b* and control region sequences. The smallest values of the minimum theoretical information criterion indicated that the Tamura & Nei (1993) substitution model (with parameters estimated from the data) was the simplest model that provided good fit for the cytochrome *b* sequences as well as for the dataset combining the cytochrome *b* and control region. Although only the neighbour-joining tree based on the Tamura & Nei (1993) model is shown (figure 2), maximum-parsimony and maximum-likelihood searches produced the same relationships among major lineages. Topology of the neighbour-joining tree (figure 2) based on divergence estimates combining the cytochrome *b* and control region sequences was similar to the cytochrome *b* tree (not shown) but with higher bootstrap support for the internal nodes. This tree demonstrates that all haplotypes from the Canadian Arctic east of Mackenzie River and Greenland (figure 1*a*) represent a monophyletic group.

There are several clades with some bootstrap support within the Canadian phylogroup (figure 2). One clade contained haplotypes distributed over a wide sector on the Canadian mainland from the Mackenzie River (locality 9) to the western coast of the Hudson Bay (locality 18; figure 1*b*). Haplotypes from Banks (localities 11 and 12), Victoria (locality 15) and Baffin Islands (locality 20) form another clade. It is notable that all eight haplotypes from the Canadian high Arctic (to the north of Parry Channel) and Greenland (figures 1*b* and 2) form a distinct lineage within the Canadian phylogroup. Although with limited bootstrap support, the high Arctic phylogroup is defined by the unique 621 A → G transition, which was found in all 23 cytochrome *b* sequences studied from the Canadian high Arctic and Greenland but not observed in the 34 other sequences sampled over the circumpolar distribution range of the genus *Dicrostonyx* (Fedorov & Goropashnaya 1999). Consistent with the cytochrome *b* data, all 78 control region sequences studied in lemmings from the Canadian high Arctic except for individuals from Prince Patrick Island (locality 25) and Greenland (locality 29) had the unique 99 G → A transition which was not observed in the 242 other control region sequences studied over the circumpolar distribution of the genus (Ehrich *et al.* 2000; V. B. Fedorov, unpublished data). Within the high Arctic clade, haplotypes from Prince Patrick Island

(locality 25) and Greenland (locality 29) represent a separate group with considerable bootstrap support.

Analysis of demographic history of the Beringian group shows modest signs of demographic expansion. The estimate of the exponential growth rate ($g = 453.0$ and 99.9% CI: 223.7–752.3) significantly exceeds zero. The Canadian phylogroup from extensively glaciated areas shows significant signs of dramatic demographic expansion with the estimate of growth rate ($g = 3655.5$ and 99.9% CI: 3369.6–3941.4) that in order of magnitude exceeds the estimate for the Beringian group. This contrast indicates that the Canadian group experienced much more substantial demographic expansion than the Beringian group in ice-free refugium.

The comparison of the log likelihoods of trees ($-\log L = 1834.5456$ and $-\log L = 1813.3794$) constructed with and without molecular clock assumption (Felsenstein 1988) shows that the cytochrome *b* sequences have evolved at roughly constant rates ($\chi^2 = 42.33$, d.f. = 32, $p > 0.05$). Therefore, variation in the cytochrome *b* gene is suitable for approximate dating of historical events. From the net nucleotide divergence (6%) between the North American and Eurasian collared lemmings (Fedorov & Goropashnaya 1999) and the first occurrence of *Dicrostonyx* fossil records in North America (1.2 Myr ago; cf. Repenning 2001), the divergence rate for the cytochrome *b* gene is estimated to be 5% per million years. It should be noted that the occurrence of lemmings in North America might have pre-dated the first fossil record. Thus, the divergence rate could be slower. However, the fast rate gives conservative time estimates. The net nucleotide divergence ($0.5 \pm 0.2\%$ (s.e.)) between the Canadian and the eastern Beringia phylogroups indicates that the main phylogenetic split across the Mackenzie River resulted from vicariant separation for about 100 000 years (95% CI: 21 000–179 000 years). The age of the most recent common ancestor within the Canadian phylogroup, on the basis of the mean within-group divergence estimate ($0.6 \pm 0.1\%$), is estimated to be 120 000 years (95% CI: 80 000–160 000 years).

Although haplotypes from the high Arctic represent a clearly defined phylogroup (figures 1*b* and 2), non-reciprocal monophyly of this group could have arisen through lineage sorting due to a founder event (Avise 2000). Therefore, the intergroup net divergence estimate may not reflect a short time of isolation of the high Arctic phylogroup from other haplotypes within the Canadian phylogroup. However, we can estimate the age of the most recent common ancestor for the high Arctic phylogroup from the mean divergence among the cytochrome *b* haplotypes within that group ($0.3 \pm 0.1\%$) to be *ca*. 60 000 years (95% CI: 20 000–100 000 years).

The neighbour-joining tree (figure 3) based on a subset of the cytochrome *b* sequences shows that the high Arctic clade was divided into two haplotype groups supported by bootstrap estimates. One phylogeographical group contains haplotypes from Prince Patrick Island (locality 25), the westernmost island of the Arctic Archipelago and eastern Greenland (locality 29). Another phylogeographical group contains all cytochrome *b* haplotypes from the central eastern part of the Canadian high Arctic Archipelago except for the haplotype from Ellef Ringnes Island (locality 26; figure 3). Notably, this group of the cytochrome *b* sequences from the central eastern part of the Canadian high Arctic Archipelago demonstrates a star-like internal topology (figure 3). Including the two cytochrome *b* sequences from each locality (except for locality 27) into the analysis, shows that there was one most common and geographically widespread haplotype (Dg7) in the centre surrounded by unique haplotypes differing by a small number (not more than 2) of synonymous substitutions (figure 3). The star-like phylogeny and low cytochrome *b* diversity in the sample from the central eastern part of the Canadian high Arctic indicate reduction in its historical effective size followed by population growth (Slatkin & Hudson 1991). This inference is supported by a significantly large negative Tajima's *D*-value (-1.94; $p < 0.05$) being indicative of population expansion (Tajima 1989). The low variation in the sample did not allow the use of the mismatch distribution analysis to estimate the timing of population expansion (Rogers 1995). However, in a bottlenecked population, the time to common ancestry, specifically post-bottleneck time (Rogers & Jorde 1995) may be estimated from nucleotide diversity ($0.066 \pm 0.028\%$) and the cytochrome *b* divergence rate as 13 200 years (95% CI: 2 200–24 200 years).

4. DISCUSSION

The division of the collared lemming into the Canadian Arctic and eastern Beringia phylogroups indicates vicariant separation followed by colonization of the Canadian Arctic from glacial refugia other than Beringia. Consistent with this, the amount of divergence between the main phylogeographical groups gives the time estimate of 100 000 years suggesting separation throughout the Wisconsin glaciation (115–10 kyr; Anderson & Borns 1997). The genetic signal of dramatic demographic expansion in the Canadian group is consistent with expansion from reduced refugial sources. However, there are two other possible explanations for the observed phylogeographical structure. First, phylogeographical division and sign of population expansion could result from a founder event during postglacial colonization of the Canadian Arctic from the eastern Beringian refugium. The average time to common ancestry (120 000 years) within the Canadian phylogroup pre-dates the last glacial maximum (18 000–22 000 years; Anderson & Borns 1997) and, thus, gives no support for a founder event with subsequent divergence during postglacial colonization from east Beringia. Second, the present phylogeographical structure could result from colonization of the Canadian Arctic by migrants from periglacial areas located to the south of the main Wisconsin ice sheets. However, this is an unlikely explanation as phylogeography of the genus *Dicrostonyx* (Fedorov & Goropashnaya 1999) implied that the two other genetically distinctive species, *D. richardsoni* and *D. hudsonius*, colonized the southeastern part of the Canadian Arctic (figure 1*a*) from areas south of the ice sheet. Thus, the main phylogeographical division in the collared lemming *D. groenlandicus* across the Mackenzie River and sign of drastic demographic expansion within the Canadian phylogroup indicate colonization of the Canadian Arctic from non-glaciated areas of limited size located to the northwest of the main ice sheet. The postglacial colonization from the northwest probably followed the eastward

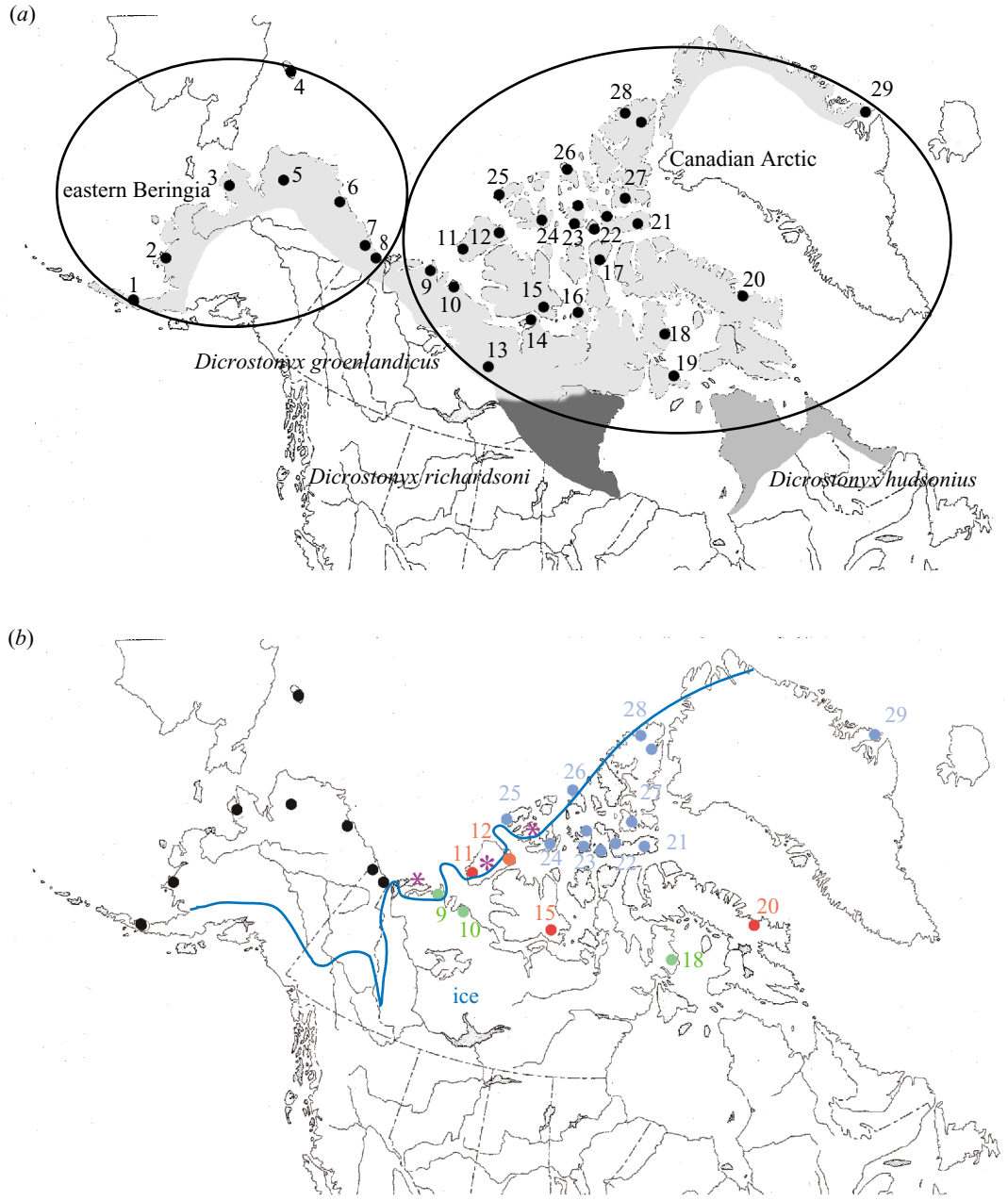

Figure 1. Map showing (*a*) species distribution (Hall 1981; Fedorov & Goropashnaya 1999), sampling localities and the geographical distribution of the main phylogeographical groups in the collared lemming, and (*b*) the geographical distribution of the phylogeographical groups in the Canadian Arctic. Each of the three pairs of localities situated close to each other on the same island (localities 21, 23 and 28) is numbered as one locality. The colour code refers to figure 2. The blue line indicates the northwest limit of the last glacial advance (Anderson & Borns 1997; Dyke *et al.* 2002). Asterisks indicate locations of the Late Pleistocene vertebrate fossils (Harington 1990) in the Canadian Arctic.

retreat of the ice front after 14 000 years (Anderson & Borns 1997).

Several clades of haplotypes supported within the Canadian Arctic phylogroup (figure 2) could result from the coalescent process within a single refugial population with large and constant historical effective size (Harpending *et al.* 1998). Therefore, taken alone this phylogeny does not necessarily indicate past isolation in several separate refugia within the Canadian Arctic. However, concordance between geographical distribution of genealogically related haplotypes and locations of possible refugia inferred from palaeoecological data may provide an insight into refugial history and colonization routes (Cruzan & Templeton 2000). Although the extent of the last glaciation in the Canadian Arctic is controversial, geological data support the existence of ice-free areas (figure 1*b*) located close to the northwest margins of the Laurentide ice sheet (Anderson & Borns 1997). Palaeoecological data are still fragmentary. However, the fossils of large grazing mammals such as saiga and muskoxen indicate extensive areas of tundra during the last glaciation on the Canadian coast to the east of the Mackenzie Delta and on western Banks

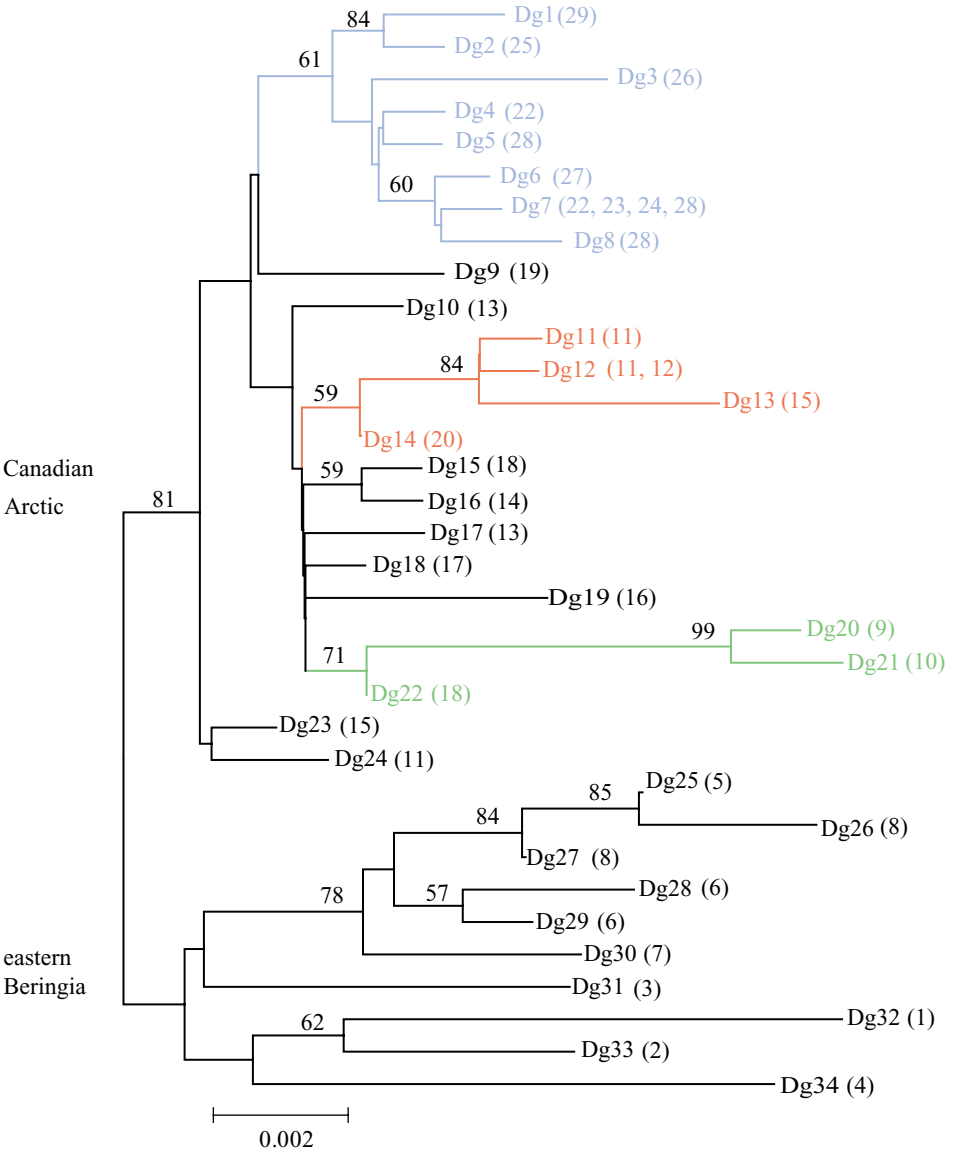

Figure 2. Neighbour-joining tree of collared lemming mtDNA sequences combining the cytochrome *b* and control region. The three clades of haplotypes from the Canadian Arctic are colour coded. Locality numbers are in parentheses and refer to figure 1. Bootstrap percentages with values greater than 50% are shown on nodes.

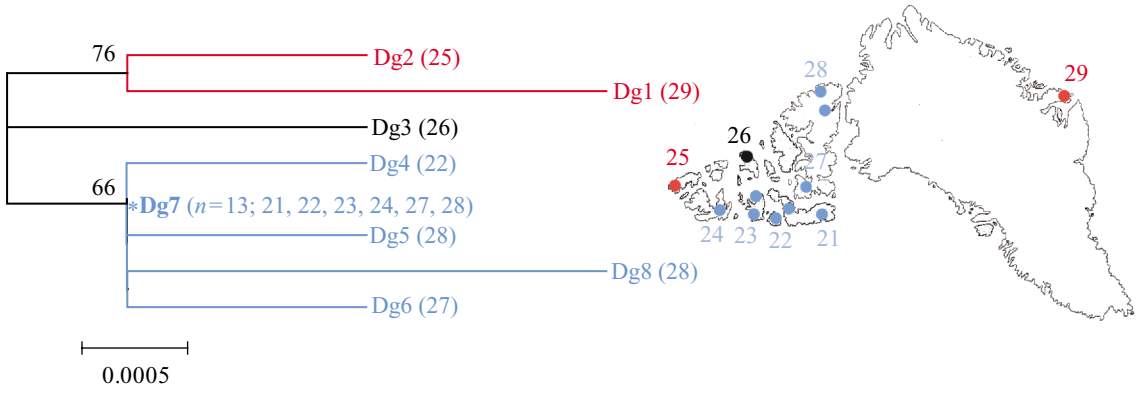

Figure 3. Neighbour-joining tree of collared lemming cytochrome *b* sequences from the Canadian high Arctic to Greenland and the geographical distribution of the phylogeographical groups. Locality numbers are in parentheses. Bootstrap percentages with values greater than 50% are shown on nodes. The most common and geographically widespread in the central eastern sector of the Canadian high Arctic, haplotype (Dg7) is in bold and designated by an asterisk.

Island (figure 1*b*; Harington 1990). Apart from the high Arctic lineage, there are two widely distributed phylogroups that possibly derived from different refugia in the Canadian Arctic (figures 1*b* and 2). The present geographical distribution of the first phylogroup might indicate postglacial eastward migration along the Canadian coast from the ice-free area at the Mackenzie Delta (locality 9) to the western coast of the Hudson Bay (locality 18). The geographical range of the second group implies colonization of formerly glaciated Victoria (locality 15) and Baffin Islands (locality 20) from non-glaciated areas on western Banks Island (localities 11 and 12).

The geographical distribution of the high Arctic phylogroup indicates colonization of deglaciated areas in the Canadian high Arctic Archipelago and Greenland from the high Arctic glacial refugia. Consistent with this, the average time to common ancestry (60 000 years) within the high Arctic clade pre-dates the last glacial maximum (18 000–22 000 years; Anderson & Borns 1997) and supports the proposal of the local glacial survival in the Canadian high Arctic and/or northern Greenland (Macpherson 1965). Two distinct clades supported within the high Arctic phylogroup (figure 3) might indicate separation in different local refugia within the Canadian high Arctic. However, it is not possible to tell from the genetic data where these refugia were located. Geological data indicate the existence of ice-free areas during the last glaciation in the western part of the Canadian high Arctic Archipelago (Dyke *et al.* 2002). Fossils of mammoth dated to the last glacial maximum (22 000 years) have been reported from Melville Island (locality 24; Harington 1990). However, vertebrate fossils available to date do not support the possibility of glacial survival in Greenland (Bennike 1997). Close affinity between haplotypes from Prince Patrick Island (locality 25) and eastern Greenland (locality 29) indicate postglacial dispersal from a single western refugium along the northwest ice margin.

The star-like cytochrome *b* phylogeny and low diversity in the sample of lemmings from the central eastern part of the Canadian high Arctic Archipelago (figure 3) provide evidence for a bottleneck event followed by population growth. The average estimate of post-bottleneck time (13 700 years) is close to the beginning of deglaciation at 14 000 years (Anderson & Borns 1997). It is feasible, therefore, that lemmings went through a bottleneck and survived the last glacial maximum in a local refugium from which migrants colonized deglaciated areas in the central eastern part of the Canadian high Arctic in postglacial times. This scenario is not excluded by geological and palaeoecological findings. Despite the recent support for the extensive Innuitian ice sheet in the central and eastern sectors of the Canadian high Arctic Archipelago (Dyke *et al.* 2002), palaeoecological findings indicate existence of a viable terrestrial ecosystem in ice-free enclaves during the last glaciation (Wolfe & King 1999).

In contrast to the traditional biogeographical view (Hultén 1937), our findings do not provide any evidence supporting significance of the eastern Beringian refugium for colonization of deglaciated areas in the North American Arctic. The phylogeographical structure in the collared lemming supports the hypothesis that, during the last glaciation, some biologically significant refugia were located in the Canadian Arctic (Macpherson 1965). Recently, several lines of evidence pointed to the possibility of the existence of glacial refugia beyond the Scandinavian ice sheet (Fedorov & Stenseth 2001; Stewart & Lister 2001). In line with these results, the present study shows that cryptic northern refugia were important sources of postglacial colonization in the North American Arctic.

We thank P. Pamilo for providing us with laboratory facilities at the Department of Conservation Biology and Genetics, Uppsala University; D. Balkwill, J. A. Cook and G. H. Jarrell for providing museum specimens; and A. V. Goropashnaya and V. L. Semerikov for advice and help in the laboratory. Many thanks to the Swedish Polar Research Secretariat for financial support and organizing the Tundra North West expedition, and to K. Fredga for support and expedition members for help during the fieldwork. This work was financially supported by grants from the Norwegian Science Council, the Nansen Endowment, University of Oslo and University of Alaska Museum.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.