Molecular Ecology (2000) **9**, 329–337

Phylogeography and mitochondrial DNA (mtDNA) diversity in North American collared lemmings (*Dicrostonyx groenlandicus*)

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Abstract

Variation in the nucleotide sequence of the mitochondrial control region (250 bp) and the cytochrome *b* region (870 bp) was examined in collared lemmings (*Dicrostonyx groenlandicus*) from 19 localities in northern Alaska and the Canadian Arctic. The division of *D. groenlandicus* in two phylogeographical groups with limited divergence across the Mackenzie River is consistent with the separation of this species in more than one refugial area located to the northwest of the Laurentide ice sheet during the last glaciation. Populations of *D. groenlandicus* from formerly glaciated areas are no less variable than those in nonglaciated areas. Instead, the low intrapopulation and intraregional diversity estimates in *D. groenlandicus* are probably a result of regional bottleneck events due to range contractions during Holocene warming events. These results are consistent with findings previously reported on collared lemmings (*D. torquatus*) from the Eurasian Arctic.

Keywords: Beringia, *Dicrostonyx*, environmental changes, glaciation, mtDNA variation, Quaternary

Received 21 June 1999; revision accepted 16 October 1999

Introduction

The glacial–interglacial periods were important events in the history of Arctic biota (Pielou 1991). The glaciations had two main effects on present patterns of genetic variation: first, geographical isolation in separate glacial refugia generated intraspecific genetic divergence (Hewitt 1996). Second, species responded to the glacial–interglacial periods by distributional changes, often associated with local extinction (Bennett 1997). The processes of distributional changes affected the geographical distribution and amount of genetic diversity. Phylogeography, the analysis of information integrating allele genealogies, geographical distribution of alleles and allele frequencies (Avise 1994), provides insight into historical factors generating extant patterns of genetic variation.

Collared lemmings (*Dicrostonyx*) are Arctic-adapted arvicoline rodents with nearly circumpolar distribution. Fedorov *et al*. (1999a) showed that vicariant separation by glacial barriers was an important factor generating intraspecific phylogeographical structure in the Eurasian *D. torquatus* (Pallas 1778). However, inconsistent with the traditional view (Sage & Wolff 1986; Hewitt 1996), the low present level of genetic diversity within geographical regions and populations of the collared lemming from the Eurasian Arctic could not be explained by a direct effect of the last glaciation. Rather the low intrapopulation and intraregional mitochondrial DNA (mtDNA) diversity in *D. torquatus* are probably a result of regional bottleneck events due to range contractions during warming events in the Holocene (Fedorov 1999; Fedorov *et al*. 1999a). The relative importance of Holocene–Pleistocene historical events for the present patterns of genetic variation in collared lemmings from the extensively glaciated American Arctic is yet unknown.

Isolation in different glacial refugia has been suggested as an important historical factor for the diversification of Arctic species in North America (Macpherson 1965; Pielou 1991). On the basis of morphological variation, Macpherson (1965) suggested that the North American collared lemming *D. groenlandicus* (Trail 1823) survived the most recent glaciation (Wisconsin; 10 000–115 000 years BP; Andersen & Borns 1997) in separate refugia. The Eastern Beringia refugium included the ice-free area in Alaska

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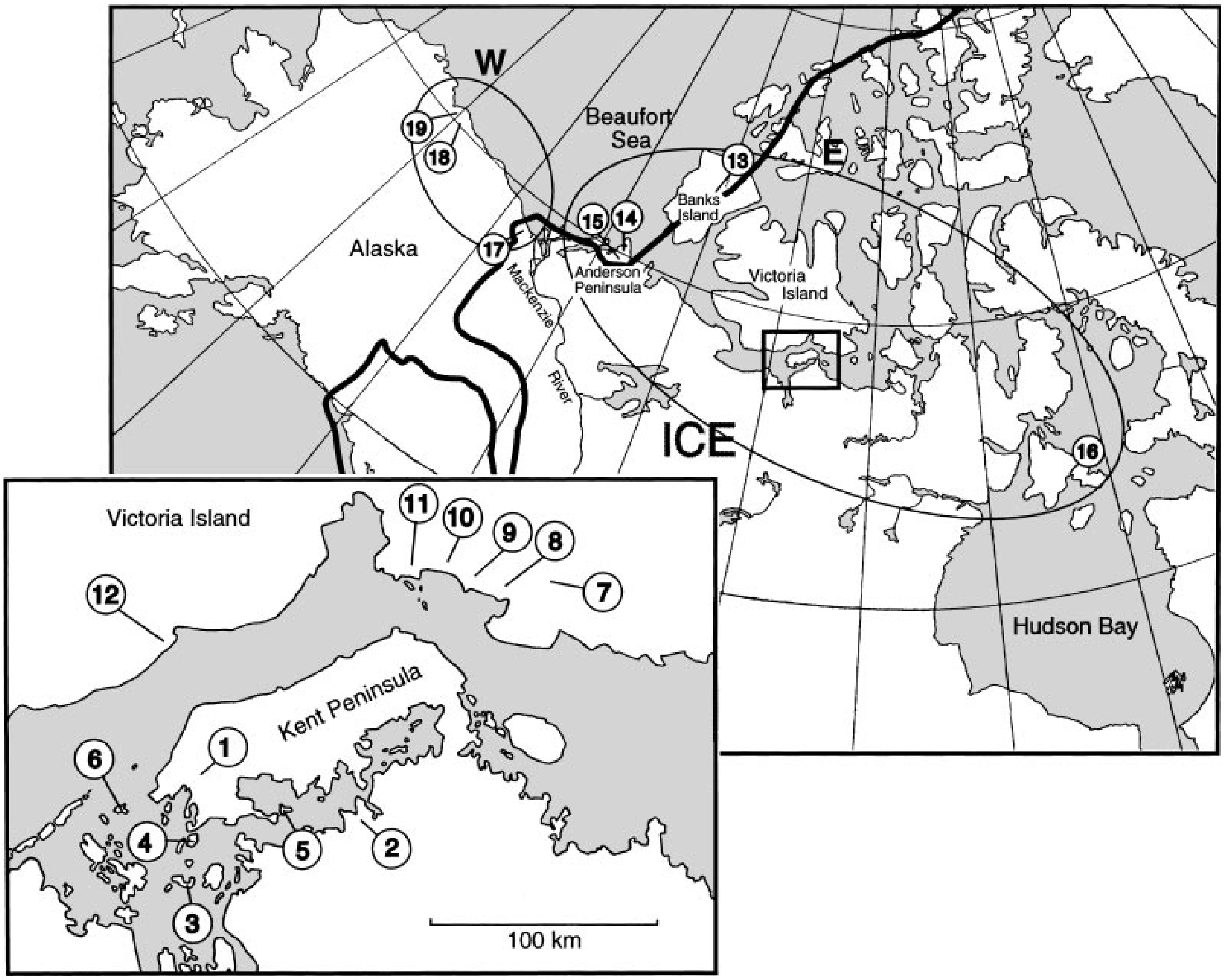

Fig. 1 Map showing the sampling localities, distribution of mitochondrial DNA (mtDNA) phylogeographical groups (W; E) in the collared lemming (*Dicrostonyx groenlandicus*), and the western limit (bold line) of the last glacial advance. The numbers on the map refer to the sites listed in Table 1.

and Canada to the west of the Mackenzie River (Fig. 1), while nonglaciated parts of the Canadian Arctic Archipelago and coastal Greenland might have contained other refugia. Refugial separation during the last glaciation could result in more than one phylogeographical group within *D. groenlandicus*. Another effect of the last glaciation on the present intrapopulation genetic diversity in the North American collared lemming can be assessed by comparing diversity estimates between nonglaciated areas in Alaska and Yukon to the west of the Mackenzie River and deglaciated areas in the Canadian Arctic (Fig. 1).

Even though environmental changes during Holocene warming events strongly affected the whole American Arctic biota (Pielou 1991), there are differences in the Holocene environmental history in different parts of the American Arctic (Edwards & Barker 1994). Pollen and plant macrofossil records indicate that forest advances to the north, in combination with sea transgressions, contracted the range of tundra communities during Holocene warm climate periods between 10 000 and 3000 years BP in the northwestern and, to a lesser known extent, in the central parts of the continental Canadian Arctic (Ritchie *et al.* 1983; Spear 1993; Payette & Lavoie 1994). In contrast, there is no evidence for Holocene forest advances and retreats in northern Alaska (Edwards & Barker 1994; Colinvaux 1996), northern Yukon (Cwynar & Spear 1995) and the Canadian Arctic Archipelago (Matthews *et al.* 1986). This contrast in the Holocene environmental history between different parts of the American Arctic makes it possible to evaluate the effect of Holocene warming events on the intrapopulation genetic diversity reflecting the demographic history of the tundra specialist

Table 1 Absolute frequencies of the control region haplotypes in 19 populations of the collared lemming (*Dicrostonyx groenlandicus*)

			Haplotypes																
	Locality	*n*	a	b	c	d	e	f	g	h	i	k	l	m	n	o	p	q	r
Kent Region	1. Walker Bay	10	10																
	2. Hope Bay	10	9	1															
	3. Breakwater	9	9																
	4. Cockburn	9	9																
	5. Hurd	10	8	1	1														
	6. Wilmot	10	10																
Victoria and Banks Islands	7. Mount Pelly	11	4		4			3											
	8. Cambridge Bay	12	2		8	2													
	9. Long Point	12	2		10														
	10. Lake Kitiga	12			10				2										
	11. Starvation Cove	13			10				1		2								
	12. Byron Bay	11	3		3			4		1									
	13. Banks Island	4			2		1				1								
Anderson Peninsula	14. North Star Harbour	11										11							
	15. Nicholson	11										11							
	16. Coral Harbour	4											4						
	17. Shingle Point	5												3	1	1			
Alaska	18. Kuparuk	10																	10
	19. Colville	10															1	4	5

D. groenlandicus, by comparing diversity estimates across geographical regions.

In this study we examined mtDNA phylogeography and diversity in the North American collared lemming (*D. groenlandicus*) from northern Alaska and the Canadian Arctic. These data were used for three purposes. First, the phylogeny was used to evaluate the hypothesis that *D. groenlandicus* was isolated in more than one refugium during the last glaciation (Macpherson 1965). Second, intrapopulation mtDNA diversity estimates in *D. groenlandicus* were compared between nonglaciated and deglaciated areas to examine the effect of the last glaciation on levels of genetic variation, specifically to evaluate the prediction that populations from formerly glaciated areas are less variable than populations from nonglaciated areas (cf. Hewitt 1996). Third, mtDNA diversity estimates were compared between geographical regions affected and regions unaffected by the Holocene tundra contractions to evaluate the effect of Holocene warming events on genetic diversity reflecting the demographic history of the tundra specialist *D. groenlandicus*. Low mtDNA diversity resulting from regional bottleneck events was expected in areas affected by the Holocene tundra contractions (Fedorov *et al*. 1999a). The comparison of our results with findings from the Eurasian Arctic allowed the elucidation of general trends in biotic responses of collard lemmings to late Quaternary environmental fluctuations on a circumpolar scale.

Materials and methods

Specimens examined

Collared lemmings (*Dicrostonyx groenlandicus*) from 19 localities in the North American Arctic were used for mtDNA analysis (Fig. 1; Table 1). In the Canadian Arctic, specimens were collected during the summers of 1996 and 1997. Specimens from Alaska (localities 18 and 19) were obtained from the Frozen Tissue Collection, University of Alaska Museum, Fairbanks. Liver and kidney tissues were sampled from snap-trapped animals and stored frozen or preserved in ethanol.

mtDNA analysis

Total genomic DNA was isolated using a phenol–chloroform extraction (Wallace 1987) or by the use of proteinase K digestion, NaCl precipitation of proteins and DNA precipitation with isopropanol (Miller *et al*. 1988). A fragment of the first hypervariable region of the mitochondrial control region (CR) (Nachman *et al*. 1994) was sequenced in 184 collared lemmings. Primers designed for the bank vole by Stacy *et al*. (1997) were used for polymerase chain reaction (PCR) amplification of the fragment which was manually sequenced according to the manufacturer's specification (Sequenase™, Amersham Life Sciences). A total of 250 bp of the CR corresponding to positions 15417–15667 in

Mus were scored for all individuals (Appendix I; EMBL Database Accession nos AF121020–AF121836). The low number of variable sites in the CR fragment (Appendix I) gave limited phylogenetic resolution in the collared lemming. For this reason a longer fragment of the mtDNA cytochrome *b* (cyt *b*) region was amplified and sequenced for eight individuals having the most common CR haplotypes within each geographical region. The cyt *b* gene was amplified by PCR and manually sequenced using a set of internal primers and a snap-cooling technique for the primer annealing as described by Fedorov *et al.* (1999b). A total of 870 bp of the cyt *b* region (EMBL Database Accession nos AJ238426–AJ238433) was scored in eight individuals of *D. groenlandicus*. For phylogenetic reconstruction, the cyt *b* and CR sequences of *D. richardsoni* (EMBL Database Accession nos AJ238435 and AF192739) were included as an outgroup.

Data analysis

To estimate divergence among haplotypes Kimura 2-parameter distances (Nei 1987) were calculated with the MEGA 1.01 program (Kumar *et al.* 1993) and neighbour-joining (NJ) phylogenetic trees were constructed from divergence estimates. Haplotype diversity (H), nucleotide diversity (π) within populations and geographical groups, and nucleotide divergence (d_A) between populations with correction for intrapopulation diversity were calculated from the CR sequences according to Nei (1987). Genetic affinities among populations were analysed by using a principal coordinate analysis based on the CR net nucleotide divergence (d_A) matrix with the NTSYS 1.8 package (Rohlf 1993). To measure the geographical subdivision of CR variation we performed an analysis of molecular variance (AMOVA; Excoffier *et al.* 1992), with a minimum number of pairwise site differences matrix as the input, using the ARLEQUIN 1.1 program (Schneider *et al.* 1997).

Results

Phylogeography of the collared lemming

Seventeen different haplotypes were found among 184 CR sequences in *Dicrostonyx groenlandicus* (Table 1). Twelve sites were variable among 250 bp scored (Appendix I). The low number of variable sites in the CR sequences provided a limited amount of phylogenetic information. The NJ tree (not shown) based on divergence estimates from the CR data showed that all haplotypes from west of the Mackenzie River (localities 17–19) form a monophyletic group. However, no clusters with considerable bootstrap support (> 70%) were defined in the CR phylogeny.

Sequencing of the cyt *b* region in eight collared lemmings selected from the main geographical regions defined by the population analysis of CR variation (see below), revealed 28 variable sites among 870 bp scored. Consistent with the CR phylogeny, the NJ tree (Fig. 2a) based on cyt *b* sequence divergence showed two groups of haplotypes with considerable support from the bootstrap test. One monophyletic group (W) includes haplotypes from northern Alaska (localities 18 and 19) and Yukon (17), while haplotypes from the Canadian Arctic (localities 1, 8, 14, and 16) form another clade (E). The division between the two phylogeographical groups is at the Mackenzie River (Fig. 1). The average divergence (d_A) between haplotype groups was 0.66% (0.48%, SE). The NJ tree (Fig. 2b) based on divergence estimates combining the cyt *b* and CR sequences produced the same two clades (E and W) with strong bootstrap support.

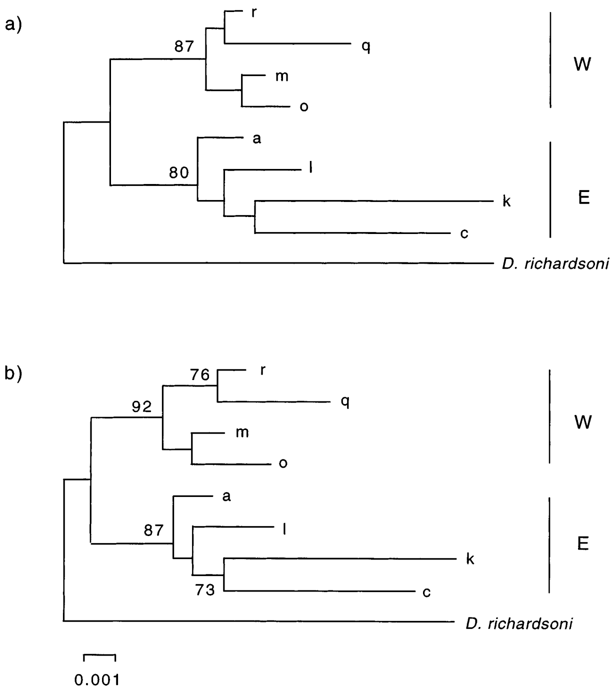

Fig. 2 Neighbour-joining (NJ) trees illustrating the phylogenetic relationships among eight selected mitochondrial DNA (mtDNA) haplotypes in the collared lemming (*Dicrostonyx groenlandicus*). Haplotypes are designated as in Table 1. The two phylogeographical groups are designated W and E and the numbers to the left of the nodes are bootstrap percentages. The tree is based on (a) divergence estimates from the cytochrome *b* (cyt *b*) sequences; (b) divergence estimates combining the control region and the cyt *b* sequences.

Genetic differentiation among geographical regions and populations in the collared lemming

Most haplotypes were specific to different geographical regions and localities (Table 1). Only Victoria/Banks

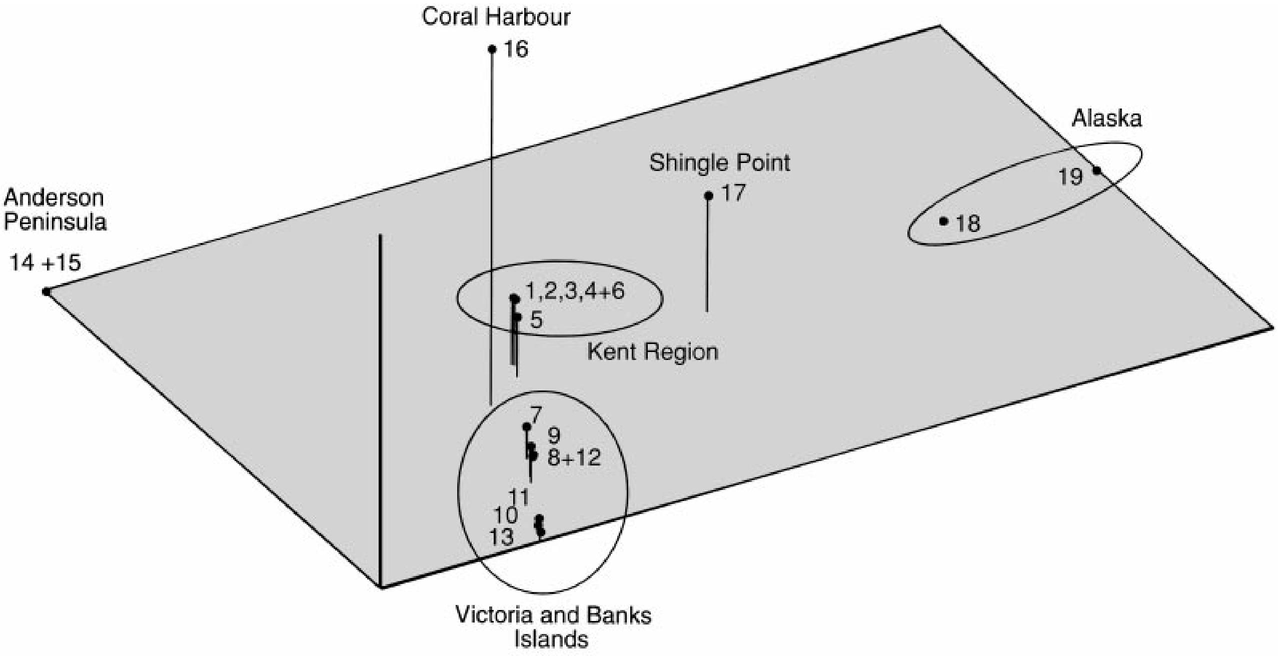

Fig. 3 Principal coordinate plot illustrating genetic affinities among the populations of the collared lemming (*Dicrostonyx groenlandicus*). The analysis is based on net interpopulation divergence estimates (d_A) from the control region sequences. Locality numbers refer to Fig. 1.

Table 2 Analysis of molecular variance based on the control region data within and among geographical regions and populations of the collared lemming (*Dicrostonyx groenlandicus*). *P*, the significance level, is the proportion of 10 000 permutation results larger than or equal to the observed estimate

Source of variation	Variance component	% of variation	*P* (equal or more extreme value)	Φ
Among regions	0.956	82.4	< 0.001	$\Phi_{RT} = 0.824$
Within regions	0.204	17.6		
Kent Region				
Among localities	−0.001	−1.9	0.756	$\Phi_{SR} = -0.019$
Within localities	0.052	101.9		
Victoria and Banks Islands				
Among localities	0.029	7.6	0.012	$\Phi_{SR} = 0.076$
Within localities	0.349	92.4		
Alaska				
Among localities	0.111	37	0.032	$\Phi_{SR} = 0.37$
Within localities	0.189	63		

Islands and Kent Region share common haplotypes (a and c). Principal coordinates analysis indicated six groupings of populations corresponding to different geographical regions (Fig. 3). The genetic distinctiveness of the geographical regions is supported by the analysis of molecular variance (Table 2) showing that most of the total mtDNA variation (82%) is allocated among regions.

Subdivision of mtDNA diversity among populations was estimated separately within each geographical region where more than one locality was sampled, excluding Anderson Peninsula where no mtDNA variation was found. Interpopulation differentiation was significant within Victoria/Banks Islands and Alaska (Table 2). However, there was no differentiation among populations within Kent Region (Table 3), as one haplotype (a; Table 1) is most common and widespread among all populations in this region.

mtDNA diversity in the collared lemming

In order to test the prediction that populations from a formerly glaciated area are less variable than populations from a nonglaciated area (Sage & Wolff 1986; Hewitt 1996), we compared intrapopulation nucleotide diversity

Table 3 Number of collared lemmings (*Dicrostonyx groenlandicus*) sampled (*n*), number of control region haplotypes observed (No. h), haplotype (*H*) and nucleotide (π) diversities and their standard deviations (SD) for each locality and total estimates for each region

Region	Locality	*n*	No. h	*H* (SD)	π in percentage (SD in percentage)
Kent Region	1. Walker Bay	10	1	0	0
	2. Hope Bay	10	2	0.20 (0.15)	0.08 (0.06)
	3. Breakwater	9	1	0	0
	4. Cockburn	9	1	0	0
	5. Hurd	10	3	0.38 (0.18)	0.16 (0.08)
	6. Wilmot	10	1	0	0
		region 58	3	0.10 (0.05)	0.04 (0.02)
Victoria and Banks Islands	7. Mount Pelly	11	3	0.73 (0.07)	0.38 (0.06)
	8. Cambridge Bay	12	3	0.55 (0.15)	0.24 (0.08)
	9. Long Point	12	2	0.30 (0.15)	0.12 (0.06)
	10. Lake Kitiga	12	2	0.30 (0.15)	0.24 (0.12)
	11. Starvation Cove	13	3	0.41 (0.15)	0.24 (0.11)
	12. Byron Bay	11	4	0.78 (0.07)	0.45 (0.07)
	13. North Banks Island	4	3	0.83 (0.22)	0.40 (0.14)
		region 75	8	0.57 (0.06)	0.29 (0.04)
Anderson Peninsula	14. Nicholson	11	1	0	0
	15. North Star Harbour	11	1	0	0
		region 22	1	0	0
	16. Coral Harbour	4	1	0	0
	17. Shingle Point	5	3	0.70 (0.21)	0.40 (0.14)
Alaska	18. Kuparuk	10	1	0	0
	19. Colville	10	3	0.64 (0.10)	0.30 (0.07)
		region 20	3	0.42 (0.12)	0.20 (0.06)

estimates across two areas with contrasting glacial histories. The nucleotide diversity estimates in populations (17–19) from ice-free areas to the west of the Mackenzie River, including Anderson Peninsula (14 and 15) and Banks Island (13), did not differ from the diversity estimates in populations (1–12, and 16) from the formerly glaciated area (Table 3; Wilcoxon two-sample test; $U = 42.5$; $P > 0.2$). In order to exclude the possible effects of Holocene environmental changes, we compared nucleotide diversity estimates in populations from glaciated (7–12 and 16) and nonglaciated (13 and 17–19) areas unaffected by the Holocene tundra contractions (see below), and found no difference (Table 3; $U = 17$; $P > 0.2$).

To examine the effect of environmental changes during the Holocene warming events on the level of mtDNA variation in *D. groenlandicus* we compared nucleotide diversity estimates between areas affected and areas unaffected by the Holocene tundra contractions. While the forest advance to the sea coast and the following retreat are well documented on Anderson Peninsula (localities 14 and 15; Ritchie *et al.* 1983; Spear 1993), the northernmost position of the Holocene tree line is controversial or unknown for the central part of the continental Canadian Arctic, including the Kent Region (localities 1–6) (cf. Payette & Lavoie 1994; MacDonald 1995). However, the Kent Region was submerged by the sea transgression about 6000 years BP (MacDonald 1995) and forest advanced to the sea coast in an adjacent area (the Coppermine River; MacDonald *et al.* 1998). Hence, it appears reasonable to regard the Kent Region as an area affected by environmental changes during the Holocene warming events. The nucleotide diversity estimates in populations (1–6 and 14–15) from geographical regions affected by the Holocene tundra contractions in the continental Canadian Arctic were lower ($U = 77$; two-tailed $P < 0.03$ with Bonferroni correction for multiple testing) than the diversity estimates in populations (7–13 and 16–19; Table 3) from northern Alaska, northern Yukon and the Canadian Arctic Archipelago, where no evidence for the Holocene forest advances was found (Matthews *et al.* 1986; Edwards & Barker 1994; Cwynar & Spear 1995; Colinvaux 1996).

On a regional scale, the occurrence of the one most common haplotype in all populations within each of the two regions (Anderson and Kent; Table 1) affected by the Holocene tundra contractions resulted in low intraregional diversity estimates (Table 3) and a lack of population structure (Table 2). As only a small amount of mtDNA variation was allocated among the population within each of two adjacent regions (Victoria/Banks Islands and Kent; Table 2) with different Holocene environmental histories, we compared total nucleotide diversity estimates across these two regions. Similar to the interpopulation comparison, the nucleotide diversity estimate on Victoria/Banks Islands exceeded the diversity estimate within the Kent Region (Table 3; Student's $t = 4.25$; two-tailed $P < 0.001$).

Discussion

Phylogeography of the collared lemming

The phylogenetic division across the Mackenzie River indicates a vicariant separation of the collared lemming (*Dicrostonyx groenlandicus*). The divergence estimate indicates that the two phylogeographical groups have been separated during the late Pleistocene (cf. Martin & Palumbi 1993). This finding does not suggest that the collared lemming recolonized deglaciated areas of the Canadian Arctic from the Eastern Beringia refugium. The phylogeographical structure supports the hypothesis that the collared lemming survived the last glaciation in at least two refugial areas (Macpherson 1965). The group of haplotypes from northern Alaska and Yukon probably represents populations from the Eastern Beringia refugium, the nonglaciated area to the west of the Mackenzie River. The phylogenetic group from the formerly glaciated Canadian Arctic to the east of the Mackenzie River was probably derived from the ice-free area on the Canadian Arctic Islands or the coastal part of northern Greenland (cf. Eger 1995). Similar to the collared lemming, the phylogeographical pattern in Arctic plant (*Dryas integrifolia*) indicates separation in two different refugia located to the northwest of the main ice sheet (Fig. 1): Beringia and the Canadian High Arctic (Tremblay & Schoen 1999). However, the possibility of glacial survival in northern Greenland is under debate (Meldgaard & Bennike 1989) and additional genetic sampling as well as fossil records are needed to reveal a complete refugial history of the collared lemming.

mtDNA diversity in the collared lemming

Inconsistent with the traditional view (Sage & Wolf 1986), populations of *D. groenlandicus* from formerly glaciated areas have no less mtDNA variation than populations in nonglaciated areas. Hence, there is no indication of reductions in effective population size due to successive bottlenecks during colonization of newly available habitats following glacial retreat (Hewitt 1996). Similar to the collared lemming, no decrease in genetic diversity in populations from deglaciated areas was reported for Arctic plants (Gabrielsen *et al*. 1997) and the Siberian lemming (*Lemmus sibiricus*) in the Eurasian Arctic (Fedorov *et al*. 1999b). Although loss of genetic diversity in northern populations has been observed in several other taxa (cf. Merila *et al*. 1997), it appears not to hold true for Arctic-adapted terrestrial organisms.

The low intrapopulation and intraregional diversity estimates in the tundra specialist *D. groenlandicus* from the areas affected by the tundra contractions suggest a reduction in long-term effective population size during warm and humid climatic events in the Holocene. This explanation is supported by the lack of mtDNA variation in the collared lemming from the Anderson Peninsula (localities 14 and 15) where the Holocene forest advances to the Beaufort Sea coast are well documented (Ritchie *et al*. 1983; Spear 1993). Similar to the American Arctic, the low intrapopulation and intraregional mtDNA diversity in the Eurasian *D. torquatus* are most probably a result of regional bottleneck events due to the northwards advances of the forest communities during the Holocene warming events (Fedorov *et al*. 1999a).

Conclusions

The results of this study are consistent with the findings from the Eurasian Arctic (Fedorov 1999; Fedorov *et al*. 1999a). The similarity between the findings from the two continents allows us to reveal the general effects of late Quaternary environmental fluctuations on the present pattern of mtDNA variation in collared lemmings (*Dicrostonyx*). The refugial isolation due to glacial barriers was an important factor generating intraspecific genetic divergence, thus, increasing genetic diversity in collared lemmings on a continental scale. However, there is no evidence for the direct effect of the last glaciation on the level of mtDNA diversity on local and regional geographical scales. Low intrapopulation and intraregional mtDNA diversity estimates in collared lemmings reflect bottleneck events which were probably a result of environmental changes during the Holocene warming periods.

Acknowledgements

The laboratory work was carried out in the DNA laboratory for systematics and ecology in the Institute of Biology, University of Oslo. The genetic analysis was funded by grants from the University of Oslo and the Norwegian Science Council (both through N.C.S.). V.B.F. and D.E. were funded by grants from the Norwegian Science Council. We acknowledge the assistance of J. Kennedy, I. Wingate, D. Wilson, and G. Gorey in the field and E. Carlson in the laboratory. We thank J. A. Cook and G. H. Jarrell for providing samples from Alaska, P. E. Jorde for valuable comments on the manuscript and R. Pienitz for help in search of palaeoecological references.

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This paper will be a part of D. Ehrich's PhD thesis on the genetic structure of fluctuating lemming populations. V. B. Fedorov is working on the phylogeography and genetic diversity of Arctic species. N. C. Stenseth's research programme focuses on the spatio-temporal variation in northern mammals. C. J. Krebs' and A. Kenney's research programme focuses on lemming dynamics, with special focus on the ecology of lemmings from the Canadian Arctic.

Appendix I Observed mitochondrial control region haplotypes in the collared lemming (*Dicrostonyx groenlandicus*). The most common haplotype, a, is taken as reference. Dots indicate identity

	Variable sites											
	101	105	114	128	130	135	168	173	174	181	215	225
a	t	t	a	c	t	c	c	c	a	t	a	g
b	.	.	.	.	.	.	.	t	.	.	.	.
c	.	.	.	.	c	.	.	.	.	.	.	.
d	.	.	.	.	c	t	.	.	.	.	.	.
e	.	.	.	.	c	.	.	.	.	c	.	.
f	.	.	.	t	c	.	.	.	.	.	.	.
g	.	.	.	t	c	.	.	.	.	.	.	t
h	.	.	.	.	c	.	.	.	.	.	.	t
i	.	.	.	.	c	.	.	t	.	.	.	.
k	.	c	.	.	.	.	.	.	.	.	g	.
l	.	.	g	.	.	.	.	.	.	.	.	.
m	a	.	.	.	.	.	.	.	.	.	.	.
n	a	.	.	.	.	.	.	.	g	.	.	.
o	a	.	.	.	.	.	.	a	g	.	.	.
p	.	.	.	.	.	.	.	.	g	.	.	.
q	.	.	.	.	.	.	t	.	g	.	.	.
r	c	.	.	.	.	.	t	.	g	.	.	.